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MANAGEMENT BRIEF

Historical Data Provide Important Context for Understanding Declines in Cutthroat Trout

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Abstract
We used historical stocking and population survey records of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* and other salmonids in the North Fork Shoshone River drainage, Wyoming to summarize fish stocking history and population trends. Based on 98 years of historical records, we found that despite extensive stocking of Yellowstone Cutthroat Trout and minimal stocking of nonnative salmonids after about 1950, populations of wild Yellowstone Cutthroat Trout declined relative to those of nonnative salmonid species. The timing of increases in nonnative salmonids (1970s) did not coincide with their period of most intensive stocking (1935–1950). It is plausible that Yellowstone Cutthroat Trout populations persisted because of high levels of supplemental stocking from 1935 to 1965 and declined with reduced stocking efforts in the 1970s, thereby allowing the increase of introduced nonnative salmonids. The establishment of nonnative salmonids likely further reduced stocking success of Yellowstone Cutthroat Trout due to competition and hybridization. This study demonstrates that an understanding of long-term stocking records and population survey data can be useful for developing and implementing successful management frameworks for the conservation of imperiled fish populations across the United States.

Cutthroat Trout *Oncorhynchus clarkii* have declined throughout the western United States (Seiler and Keeley 2009; Gresswell 2011). Population declines are linked to climate change (Gresswell 2011), competition (Kruse 1998;

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Kruse et al. 2000; Peterson et al. 2004; Gresswell 2011), predation (Gresswell 1995, 2011; Ruzycki et al. 2003), and hybridization with introduced salmonid species (Kruse 1998; Allendorf et al. 2001; Weigel et al. 2003; Muhlfeld et al. 2009; Kovach et al. 2011; Love Stowell et al. 2015). The stocking of nonnative salmonids is likely an important contributor to wideranging Cutthroat Trout declines in western North America and is thought to be a primary explanation for the loss or extirpation of native fish faunas (Rahel 2000, 2002; Pister 2001).

Intensive stocking of native and introduced species of salmonids in the United States began in the 1800s (Pister 2001; Halverson 2010). Initially, stocking was used as a way to support westward expansion and provide sustenance for settlers; stocking for recreational purposes developed considerably later (Pister 2001; Rahel 2016). Over the past five decades, efforts from fisheries management agencies have shifted from stocking nonnative salmonids for recreation to stocking native species for conservation (Peterson et al. 2004; Gresswell 2011).

Understanding historical stocking practices is necessary for better understanding the context for population declines and prospects for conservation (Metcalf et al. 2012; Loxterman et al. 2014; Muhlfeld et al. 2017). However, historical data sets are still underused, in part due to the challenges that are associated with their availability and the labor-intensive aspects of digitizing older records. In this study, we paired historical stocking records for multiple native and nonnative species with historical survey data to better understand the context for declines of native Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in the North Fork Shoshone River, Wyoming, USA. We used long-term stocking and population survey data for the North Fork Shoshone River drainage to assess and provide context for declines in Yellowstone Cutthroat Trout populations within this drainage. Our objective was to document and compare historical stocking trends between native and nonnative salmonid species. We use historical stocking and abundance trends to discuss potential hypotheses for Yellowstone Cutthroat Trout declines and management implications.

METHODS

Study Location

All of the summarized stocking events occurred in the North Fork Shoshone River drainage, located in the northwest corner of Wyoming, in the Absaroka Mountain Range, west of Cody, Wyoming and just east of Yellowstone National Park (Figure 1). The North Fork Shoshone River drains into Buffalo Bill Reservoir, which was constructed in 1910. The total drainage area is 913 square miles (Kent 1973). The main stem of the North Fork Shoshone River is approximately 50 miles in length. In the upper 40 miles, the river flows through the Shoshone National Forest, and in the lower 10 miles, the river flows through private land before entering Buffalo Bill Reservoir (Figure 1). Populations of wild Yellowstone Cutthroat Trout were present in the North Fork Shoshone River prior to the onset of stocking, which likely began because of increased fishing pressure (Gresswell 2011). It is unclear to what extent current populations are the descendants of original wild populations or the descendants of stocked fish; genetic investigations on this subject are ongoing.

Historical Stocking and Survey Records

The Cody Regional office of the Wyoming Game and Fish Department provided historical stocking records for the North Fork Shoshone River drainage. We summarized 98 years of historical records starting in 1911 and ending in 2009. It is likely that additional undocumented stocking events occurred before 1911 and throughout the 98 years of documented stocking events. There has been some limited Yellowstone Cutthroat Trout stocking post 2009, but it was excluded from our assessment because it only occurred in two isolated ponds in the North Fork Shoshone River drainage (Messamer 1984). See Supplemental Material for historical fish stocking and population survey records (available in the online version of this article).

The historical stocking and population survey data came from 27 locations (Table 1; Figure 1). These included 25 tributaries that feed the North Fork Shoshone River,

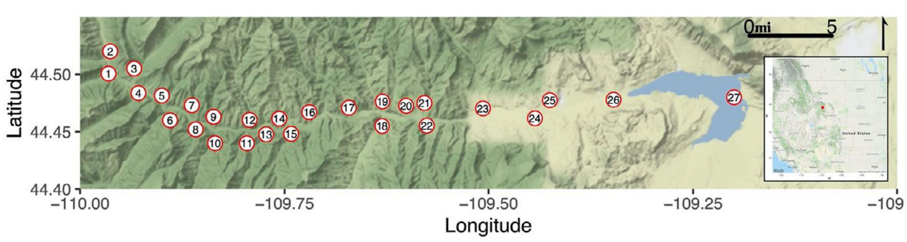

FIGURE 1. Map of the North Fork Shoshone River drainage. There were 27 locations where historical fish stocking and population surveys occurred. The sites are numbered as shown in Table 1. The map numbers do not show the precise locations of where the historical fish stocking and survey events occurred. Multiple fish-stocking and survey events have occurred at each location, but the precise locations were not documented in the historical records. [Color figure can viewed at afsjournals.org.]

TABLE 1. Recorded locations of historical fish stocking and population surveys for the North Fork Shoshone River drainage. The total number of fish stocked varied by location. Historical fish stocking and survey events occurred at multiple locations for each site; however, the precise locations were not given in the historical records. The asterisks denote locations where the historical stocking records were not available, but there were historical population survey records. The map numbers correspond to the 27 locations shown in Figure 1 and are used for the ease of viewing.

Location	Total number of fish stocked	Tributary vs. main stem	Map number
Middle	497,678	Tributary	1
North Fork Shoshone	2,318,148	Main stem	2
Grinnell	213,382	Tributary	3
Canfield*	–	Tributary	4
Mormon	20,000	Tributary	5
Eagle	263,642	Tributary	6
Libby	35,574	Tributary	7
Kitty	251,942	Tributary	8
Goff	56,092	Tributary	9
Fish Hawk	172,530	Tributary	10
Mesa*	–	Tributary	11
Gunbarrel	178,192	Tributary	12
Sheep*	–	Tributary	13
Newton	93,698	Tributary	14
Blackwater	122,322	Tributary	15
Moss	115,000	Tributary	16
Clearwater	1,280	Tributary	17
Elk Fork	470,258	Tributary	18
Sweetwater	138,391	Tributary	19
Horse	133,100	Tributary	20
Grizzly*	–	Tributary	21
Clocktower*	–	Tributary	22
Big	65,000	Tributary	23
Whit*	–	Tributary	24
Jim*	–	Tributary	25
Trout	98,831	Tributary	26
Buffalo Bill Reservoir	11,602,043	Main stem	27

the entire main stem of the North Fork Shoshone River, and Buffalo Bill Reservoir. Historical stocking and population surveys occurred at multiple locations for each site; however, the precise locations were not given in the historical records. Historical survey data for the tributaries and the main stem were collected primarily by using backpack and boat electrofishing. Buffalo Bill Reservoir was surveyed primarily using gill nets. The other survey methods that were used included creel surveys, rod and line, seine and trap nets, visual estimates, and dynamite. The historical stocking and survey records included information for dates, locations, fish species, number of species, average lengths, average weights, hatchery locations, sampling techniques, air temperatures, and water temperatures. The data formats were inconsistent across stocking events, and records for some stocking events are incomplete. For example, some stocking records list only a year or range of years, not month or date. Other stocking records list a complete date but no information about the size of the fish that were stocked. For each summary, we included as much of the data as possible but were forced to exclude stocking events with missing data in focal fields.

Species of Interest

We focused primarily on the stocking and population survey history of Yellowstone Cutthroat Trout and Rainbow Trout *Oncorhynchus mykiss* because there is considerable evidence for native Cutthroat Trout population declines caused by hybridization, both in this drainage and elsewhere (Allendorf et al. 2001; Muhlfeld et al. 2009). A subset of data on Yellowstone Cutthroat Trout and Rainbow Trout stocking was previously used to provide context for a genetic study of hybridization (Mandeville et al. 2019), but temporal trends have not been previously summarized. We also described the stocking and population survey history of other salmonids, specifically Brook Trout *Salvelinus fontinalis* and Snake River Cutthroat Trout *O. clarkii behnkei*. Though not clearly genetically distinct from Yellowstone Cutthroat Trout, Snake River Cutthroat Trout does differ in ecology and morphology and has been managed separately in Wyoming (Trotter et al. 2018). The historical records used several names to classify Cutthroat Trout, including "Cutthroat," "Blackspotted," "Yellowstone Cutthroat," and "Snake River Cutthroat." The historical management reports suggest that all of the Cutthroat Trout that were stocked before 1957 were Yellowstone Cutthroat Trout (Kent 1973); therefore, all entries only stating "Cutthroat" or "Blackspotted" prior to 1957 were classified as Yellowstone Cutthroat Trout. Furthermore, three stocking events classified the species stocked as "Native." Because Yellowstone Cutthroat Trout were the only native trout that were cultured at the time, we assumed that this referred to Yellowstone Cutthroat Trout.

The other species that were stocked included Brown Trout *Salmo trutta*, Lake Trout *Salvelinus namaycush*, Arctic Grayling *Thymallus arcticus*, and Mountain Whitefish *Prosopium williamsoni* (translocation). However, we did not focus on the stocking of these species because they were stocked either primarily within Buffalo Bill Reservoir or infrequently.

Data Summarization

All of the summaries were completed using R (R Core Team 2018). We calculated the total number of individuals stocked and relative abundances for each species from survey data that were obtained between 1911 and 2009. For each species, we summed total number of individuals that were stocked both over the entire period of our data set and by year. We also quantified what proportion of sampled individuals each species comprised in each year with survey data. The historical survey sampling methods varied from year to year, but they remained relatively consistent across the sampling locations. Inconsistencies in sampling gear or method may have affected the results for capture probability, but specific sampling uncertainties and objectives could not be identified based on the given records.

To understand how stocking practices varied across species, we compared season of stocking (month) across the four most commonly stocked salmonid species: Yellowstone Cutthroat Trout, Rainbow Trout, Brook Trout, and Snake River Cutthroat Trout. We also compared size at stocking, using a Welch's two sample *t*-test, for all of the species except Snake River Cutthroat Trout, for which no length data were available. For Yellowstone Cutthroat Trout, we also examined trends in the length and weight of the stocked fish through time.

TABLE 2. Total number and percentage of fish stocked in the North Fork Shoshone River drainage by species. There were approximately 16.8 million fish stocked within this drainage between 1911 and 2009. Of the four salmonid species of interest, Yellowstone Cutthroat Trout were proportionally stocked the most and Rainbow Trout were proportionally stocked the least.

Species stocked	Number of fish stocked	Proportion of total fish stocked
Yellowstone Cutthroat Trout	13,498,904	0.801
Snake River Cutthroat Trout	983,004	0.058
Brook Trout	921,718	0.055
Lake Trout	794,818	0.047
Rainbow Trout	446,126	0.026
Arctic Grayling	200,000	0.012
Brown Trout	2,302	<0.001
Mountain Whitefish	2,31	<0.001
Total fish stocked	16,847,103	

RESULTS

Between 1911 and 2009, a total of 16,847,103 individual fish were stocked throughout the North Fork Shoshone River drainage (Table 2). Of the total number of fish that were stocked over the 98 years of historical stocking records, 86% were Cutthroat Trout. Yellowstone Cutthroat Trout were proportionally stocked the most, at 80% of stocked fish (Table 2; Figure 2B), followed by Snake River Cutthroat Trout at 6%. The other species that were stocked were Brook Trout at 5%, Lake Trout at 5%, Rainbow Trout at 3%, Arctic Grayling at 1%, and Brown Trout and Mountain Whitefish at less than 1%.

Yellowstone Cutthroat Trout were stocked 592 times between 1911 and 2009 (Table 3; Figure 2A). Snake River Cutthroat Trout were stocked intensively for a short period: 156 times between 1969 and 1980. Brook Trout were stocked 100 times between 1911 and 1951 and Rainbow Trout 26 times between 1911 and 1962. Yellowstone Cutthroat Trout comprised the greatest proportion of fish that were stocked, except in the 1970s when it was Snake River Cutthroat Trout (Table 2; Figure 2B).

The relative abundance of Rainbow Trout increased rapidly in the late 1970s, substantially after their final recorded stocking event in 1962 (Figure 2C). In contrast, the relative abundance of Yellowstone Cutthroat Trout decreased in the late 1970s despite being continually stocked into the 2000s and being the overwhelming majority of fish that were stocked throughout the 98 years of stocking records. Low abundances of Yellowstone Cutthroat Trout × Rainbow Trout hybrids were recorded between 1960 and 2009. Snake River Cutthroat Trout were occasionally found during historical surveys that were conducted between 1969 and 1980. Brook Trout were rarely recorded in the historical survey records.

Similar patterns in when and what species were being stocked were seen across stocking locations (Figure 1; Figure 3). The number of individuals and number of stocking events that were recorded for Buffalo Bill Reservoir and the river main stem were substantially greater than those that were recorded for the individual tributaries (Figure 3).

Yellowstone Cutthroat Trout were generally stocked at smaller sizes than were Rainbow Trout or Brook Trout. Yellowstone Cutthroat Trout had a median size at stocking of 1.72 in (Figure 4A), compared with Rainbow Trout at 2.25 in (Figure 4B) and Brook Trout at 3.04 in (Figure 4C). The pairwise differences in stocking length were significant for all of the comparisons between these three species (*t*-tests: Yellowstone Cutthroat vs. Rainbow trout $P < 2.2 \times 10^{-16}$; Yellowstone Cutthroat vs. Brook Trout, $P < 2.2 \times 10^{-16}$; Rainbow Trout vs. Brook Trout, $P < 2.2 \times 10^{-16}$). The lengths for Snake River Cutthroat Trout were not included in the historical stocking records.

Overlaps in stocking season were seen between all of the salmonid species (Figure 5). Yellowstone Cutthroat Trout were primarily stocked during August through September, but the stocking season extended from February to November (Figure 5A). Rainbow Trout stocking season extended from June to September, with the highest stocking rates occurring in September (Figure 5B). Brook Trout were stocked during March through September,

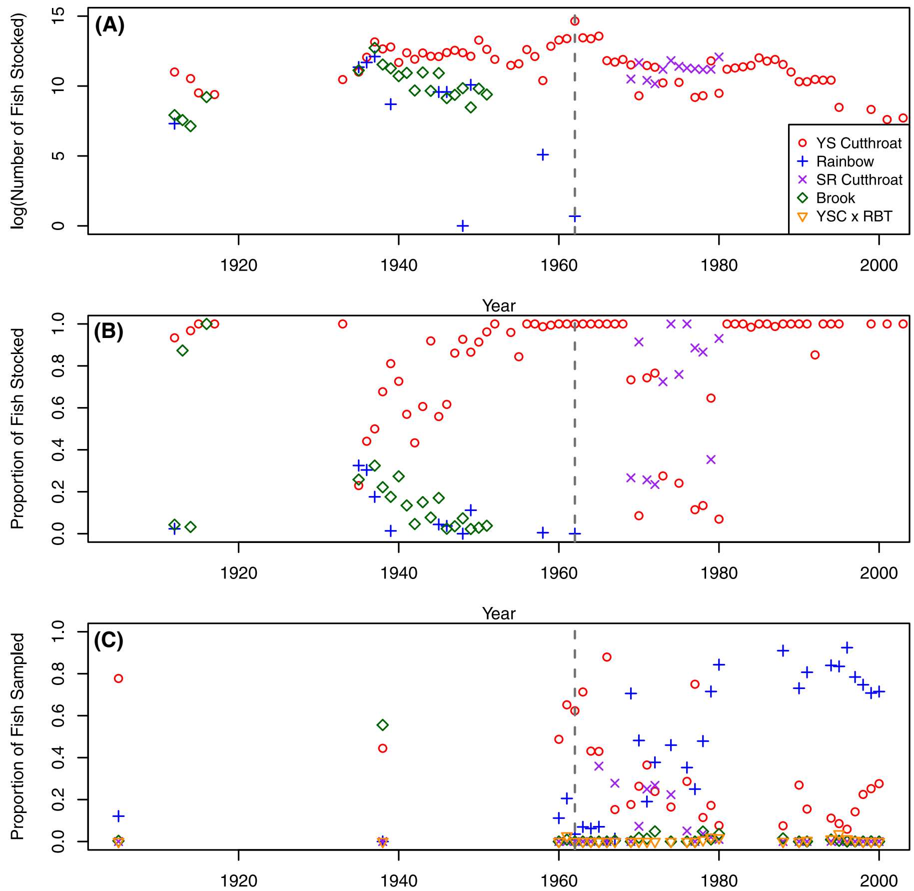

FIGURE 2. **(A)** Total number of individuals of each species stocked in the North Fork Shoshone River drainage from 1911 to 2009. The totals were summed across all of the tributaries, the main stem of the North Fork Shoshone River, and Buffalo Bill Reservoir. Panel **(B)** shows the proportion of the total number of fish stocked for each species from 1911 to 2009, and panel **(C)** shows the proportion of fish sampled in the population surveys for each species plus Yellowstone Cutthroat Trout × Rainbow Trout hybrids from 1911 to 2009. For all of the panels, the gray dashed line denotes the last year when Rainbow Trout were stocked. YS Cutthroat and YSC = Yellowstone Cutthroat Trout; SR Cutthroat = Snake River Cutthroat Trout; RBT = Rainbow Trout. [Color figure can viewed at afsjournals.org.]

TABLE 3. Total number of stocking events and stocking period for each fish species of interest over a 98-year period. Yellowstone Cutthroat Trout were stocked the most frequently and for the longest duration. Rainbow Trout had the fewest stocking events.

Species of interest	Total stocking events	Stocking time frame
Yellowstone Cutthroat Trout	592	1911 to 2009
Snake River Cutthroat Trout	156	1969 to 1980
Brook Trout	100	1911 to 1951
Rainbow Trout	26	1911 to 1962

with the highest rates occurring in July (Figure 5C). Snake River Cutthroat Trout were primarily stocked during March through May, but stocking lasted from March through October (Figure 5D).

We compared size at stocking through time only for Yellowstone Cutthroat Trout because this was the species with the greatest number of stocking events. The length data extended only to 1965, and for that period there was no significant trend (Figure 6A). The average weights of Yellowstone Cutthroat Trout that were stocked increased sharply in the 1960s and 1970s before declining later (Figure 6B).

DISCUSSION

In this study, we contextualized the decline of a native Cutthroat Trout subspecies, Yellowstone Cutthroat Trout, by completing a detailed assessment of the history of fish stocking in the North Fork Shoshone River drainage, Wyoming. Overall, there was a mismatch between stocking and trends in relative abundance.

Despite extensive stocking efforts for Yellowstone Cutthroat Trout, their relative abundance declined and

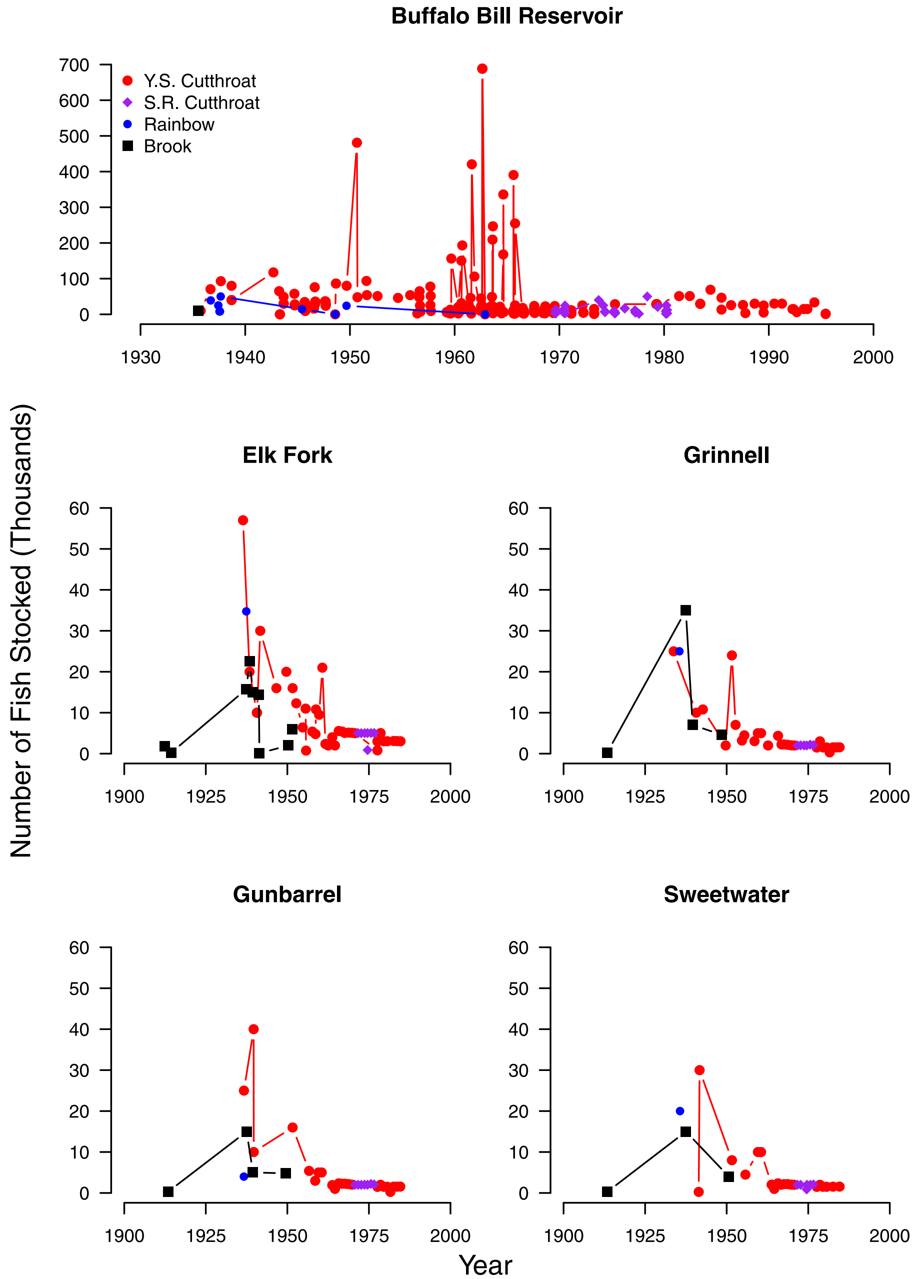

FIGURE 3. Number of fish stocked of each species between 1911 and 2009 for a subset of representative locations in the North Fork Shoshone River drainage. Shown above are Buffalo Bill Reservoir and four tributaries of the North Fork Shoshone River upstream of Buffalo Bill Reservoir. Although the magnitude of stocking was much higher in Buffalo Bill Reservoir, similar trends in the species that were being stocked and when they were being stocked across all locations can be seen. Y.S. Cutthroat = Yellowstone Cutthroat Trout; S.R. Cutthroat = Snake River Cutthroat Trout; Rainbow = Rainbow Trout; Brook = Brook Trout. [Color figure can viewed at afsjournals.org.]

Rainbow Trout populations increased in the 1970s. This is surprising, as Rainbow Trout were stocked substantially less often and at much lower numbers (Table 2; Figure 2A, 2B); additionally, Rainbow Trout were primarily stocked in only a subset of the basin, in Buffalo Bill Reservoir (see Figure 1). It is unclear why this relatively sudden shift in species composition occurred in the 1970s despite the cessation of Rainbow Trout stocking over 10 years prior and massive supplemental stocking of Yellowstone Cutthroat Trout. We advance several possible explanations for the historical decline of Yellowstone Cutthroat Trout, including (1) competition with introduced

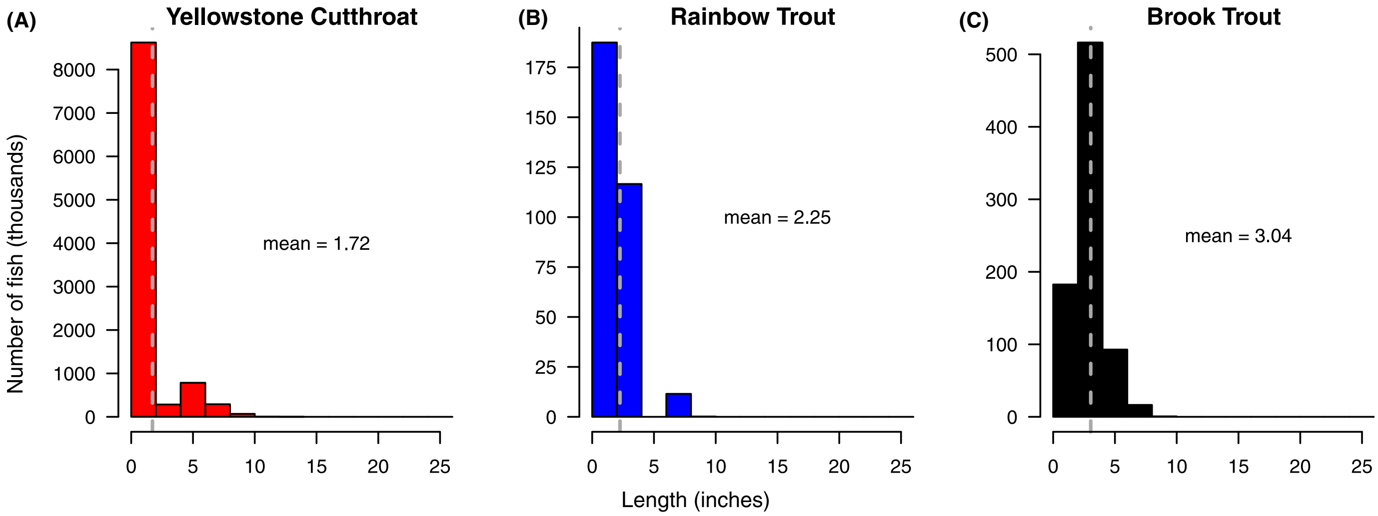

FIGURE 4. Lengths of individual species of interest stocked between 1911 and 1965. Panels **(A–C)** show the average lengths of Yellowstone Cutthroat Trout, Rainbow Trout, and Brook Trout, respectively. The lengths for Snake River Cutthroat Trout were not included in the historical stocking records, so we were not able to compare them with the other species. [Color figure can viewed at afsjournals.org.]

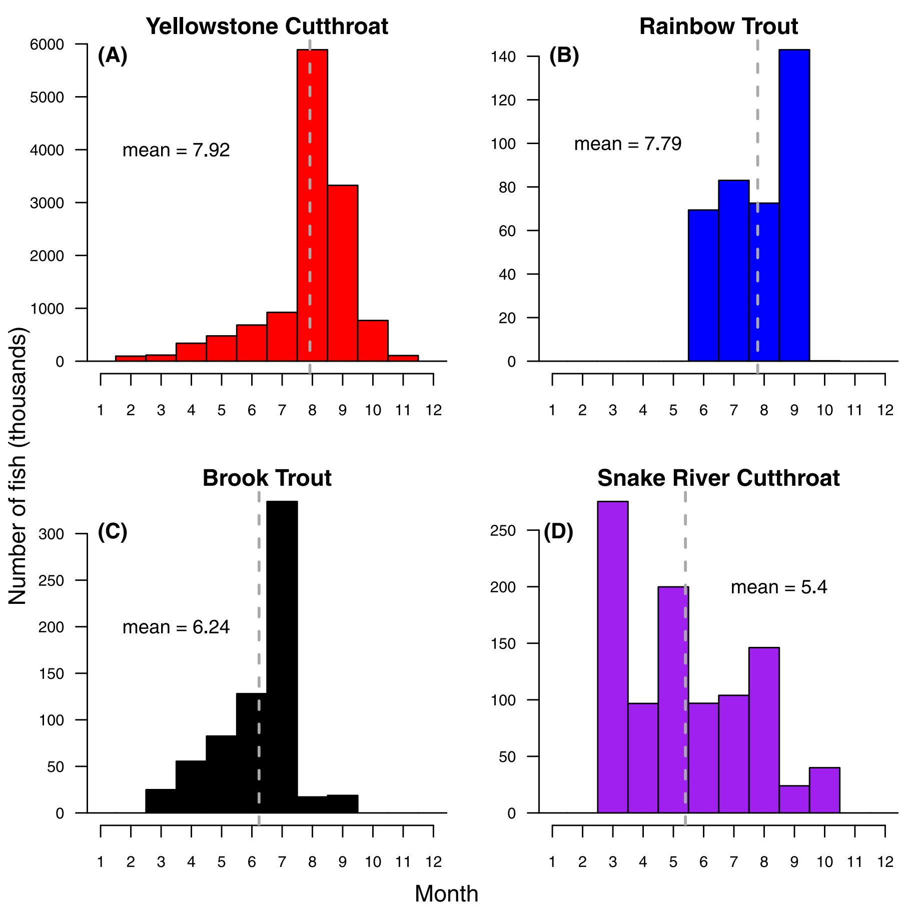

FIGURE 5. Month of stocking for individual species of interest stocked between 1911 and 2009. Panels **(A–D)** show the average month of stocking for Yellowstone Cutthroat Trout, Rainbow Trout, Brook Trout, and Snake River Cutthroat Trout, respectively. [Color figure can viewed at afsjournals.org.]

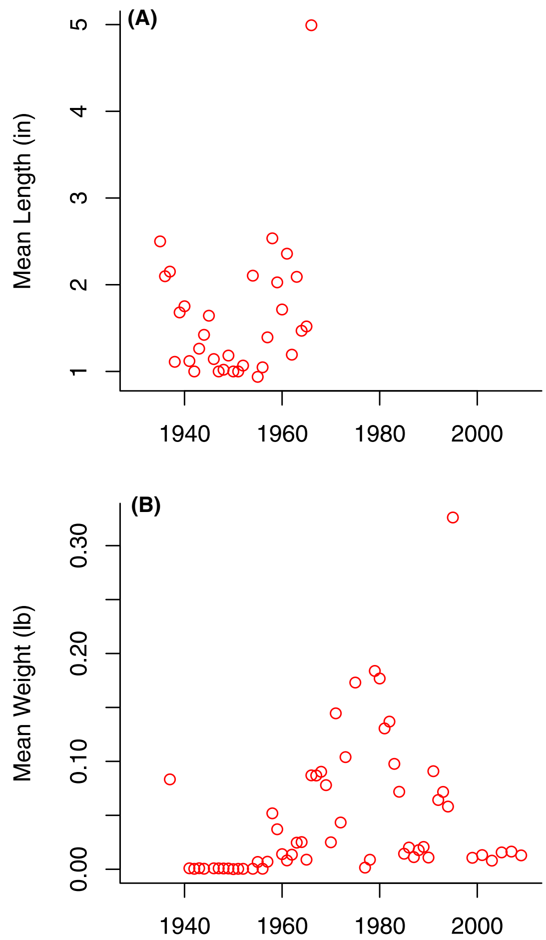

FIGURE 6. Average **(A)** lengths and **(B)** weights of stocked Yellowstone Cutthroat Trout individuals by year. Length data were unrecorded after 1965. Lengths and weights were not recorded at every stocking event; stocking events where these data were not recorded are excluded from these plots. [Color figure can viewed at afsjournals.org.]

salmonids, (2) hybridization, and (3) shifts in stocking practices. These explanations are not entirely independent of one another, and we suspect that some combination of these processes caused the decline of Yellowstone Cutthroat Trout in the North Fork Shoshone River basin.

Competition

In the North Fork Shoshone River, limited habitat segregation among Yellowstone Cutthroat Trout, Brook Trout, and Rainbow Trout has potentially led to competitive interactions for critical spawning habitat and food resources (Kruse 1998; Gresswell 2011). In many systems, Brook Trout exclude native Cutthroat Trout populations through niche overlap and competitive exclusion (Kruse et al. 2000, 2001; Shepard et al. 2002; Novinger and Rahel 2003; Peterson et al. 2004; Gresswell 2011). Although relatively few Brook Trout were stocked into the North Fork Shoshone tributaries (Table 2; Figure 2), populations have become established in several tributaries. Their introduction may have weakened native Yellowstone Cutthroat Trout populations and removed the potential for headwater refuge of Cutthroat Trout (Young et al. 2017). Cutthroat Trout populations are also frequently displaced by nonnative Rainbow Trout (Peterson et al. 2004; Shepard 2004; McGrath and Lewis 2007; Seiler and Keeley 2009; Halverson 2010; Gresswell 2011).

Competitive advantages can be influenced by length, weight, and timing of stocking. We found considerable overlap in timing of stocking, highlighting the potential for priority effects or competition (Figure 2B; Figure 5). Rainbow Trout and Brook Trout were commonly stocked at larger sizes than were Yellowstone Cutthroat Trout (Figure 4), which could have led to the suppression of Yellowstone Cutthroat Trout fry growth and establishment success (Fausch 1988). Fish stocked at larger body lengths and weights may have a competitive advantage, as they are better able to avoid predation and obtain resources more efficiently (Biro et al. 2004; Hyvärinen and Vehanen 2004). However, the idea that stocking at larger sizes leads to better survival or growth remains controversial; an opposing body of evidence suggests that hatchery acclimation tends to have mostly negative effects and that fish stocked earlier and at smaller sizes are more successful (Stringwell et al. 2014; LeCheminant 2019). Interestingly, the period of Yellowstone Cutthroat Trout decline (1970s) corresponds to when these fish were likely stocked at larger sizes, based on weight estimates (Figure 6B).

Hybridization

Hybridization between native Cutthroat Trout and introduced Rainbow Trout is a common mechanism for the displacement of native Cutthroat Trout populations (McGrath and Lewis 2007; Gresswell 2011). In the North Fork Shoshone River drainage, Yellowstone Cutthroat Trout declines coincided with Rainbow Trout increases and extensive hybridization between these two species has been observed (Kruse 1998; Kovach et al. 2011; Mandeville et al. 2019). Low numbers of Yellowstone Cutthroat Trout × Rainbow Trout hybrids were recorded between 1960 and 2009, though it is likely that a larger hybrid population was present but not identified (Figure 2C). Hybrid offspring can have lower fitness than parental individuals, but in Westslope Cutthroat Trout × Rainbow Trout crosses, if the first generation of hybrids is sufficiently fit, multiple generations of hybridization typically occur in spite of the negative fitness consequences (Allendorf and Leary 1988; Muhlfeld et al. 2009). Hybridization potentially eliminates native populations through admixture; moreover, the presence of hybrid offspring can lower native Cutthroat Trout growth rates, developmental stability, and reproductive success (Allendorf and Leary 1988; Muhlfeld et al. 2009; Seiler and Keeley 2009). Hybridization can also have negative demographic consequences, as hybridization occurs at the expense of conspecific reproduction, potentially leading to population declines (Wolf et al. 2001). Therefore, it is possible that native Yellowstone Cutthroat Trout declines in the North Fork Shoshone River drainage were because of the demographic or fitness consequences of hybridization or both.

Stocking Practices

Shifts in stocking practices, including source population, season of stocking, and size at stocking, could have contributed to the declines in native Yellowstone Cutthroat Trout, especially if stocking hatchery-reared Yellowstone Cutthroat Trout maintained populations between 1911 and 1970 but did not successfully restore a persistent population of wild Yellowstone Cutthroat Trout. In the 1970s, managers switched to stocking Snake River Cutthroat Trout due to the unavailability of Yellowstone Cutthroat Trout (Messamer 1984; J. C. Burckhardt, Wyoming Game and Fish Department, personal communication). This switch was then followed by the swift population decline of Yellowstone Cutthroat Trout and population increase of Rainbow Trout (Figure 2C), although it is unclear whether there is any causal link between these events. Yellowstone Cutthroat Trout stocking resumed in the late 1970s and early 1980s, but it was discontinued in 1991 following a Wyoming Game and Fish Department policy of supporting wild trout in Wyoming streams (Kent 1995).

Stocked Yellowstone Cutthroat Trout may not have been able to successfully establish naturally reproducing populations despite sustained stocking for several reasons. It is possible that hatchery-raised fish had low survival and reproductive success, and when population supplementation through continued stocking decreased or involved suboptimal hatchery fish, populations began to decline. It is unclear how supplementing wild Yellowstone Cutthroat Trout populations with hatchery fish might have affected the reproduction of the preexisting wild populations in this system. However, a study completed on the Madison River, Montana shows that stocking catchable-sized trout reduced the number of wild trout populations and the cessation of stocking resulted in significant increases in wild trout populations and biomass (Vincent 1987). Interbreeding of hatchery and wild fish may have lowered offspring fitness, as fish with recent hatchery origins often have lower fitness than do native or naturalized individuals of the same species (Araki et al. 2007). In addition, local adaptation plays a key role in the reproductive success of many native, wild Cutthroat Trout populations (Carim et al. 2017). Fish from Yellowstone Lake and other sources were stocked into the North Fork Shoshone River basin. These stocked fish might not be well adapted to the cold, steep streams in the North Fork Shoshone River basin, which flow down out of the Absaroka Mountains and thus represent a fundamentally different habitat type than that encountered in Yellowstone Lake.

Other Considerations

Variation in environmental conditions could have played an important role in failure of stocked Yellowstone Cutthroat Trout to persist despite extensive stocking. Yellowstone Cutthroat Trout populations thrive in coldwater environments, and warmwater conditions are associated with decreased survival, growth, and reproduction (Gresswell 2011). Over the past century, there have been two primary periods of warming throughout the native range of Yellowstone Cutthroat Trout, including in the North Fork Shoshone River drainage: 1910 to 1945 and 1976 to present (Gresswell 2011; Al-Chokhachy et al. 2013). Periods of warming could have enabled the expansion of Rainbow Trout and other salmonids after the 1970s within the drainage.

Angler harvest could also have contributed to Yellowstone Cutthroat Trout declines. Stocking was likely initiated in the North Fork Shoshone River drainage due to declines of wild Yellowstone Cutthroat Trout as a result of angler harvest (Gresswell 2011). The vulnerability of Yellowstone Cutthroat Trout to angling pressure is thought to be relatively high compared with that of other salmonid species (MacPhee 1966; Schill et al. 1986; Gresswell 1995; Gresswell and Liss 1995). Exploitation may also have reduced stocking success, as hatchery-reared fish are more susceptible to angler harvest compared with wild populations due to differences in feeding and predator-avoidance behavior (Härkönen et al. 2014). Therefore, the Yellowstone Cutthroat Trout populations that were stocked in the North Fork of Shoshone River drainage were likely vulnerable to angler fishing pressure and being harvested in large numbers (Rahel 2016).

Management Implications

Summarizing these historical stocking records provides important context for current management actions. Managers acknowledge that Rainbow Trout are one of the greatest threats to the long-term persistence of Yellowstone Cutthroat Trout because of hybridization (Kruse 1998; May et al. 2007; Kovach et al. 2011; Mandeville et al. 2019). Currently, the North Fork Shoshone River drainage is dominated by Rainbow Trout and Yellowstone Cutthroat Trout × Rainbow Trout hybrids (Mandeville et al. 2019). Reestablishing productive Yellowstone Cutthroat Trout populations in this drainage would likely require the suppression or eradication of nonnative trout. Given the history that is outlined in the paper, it is unclear whether stocking Cutthroat Trout would be effective for restoring Cutthroat Trout populations, but we caution that appropriately choosing a broodstock would be a critical challenge, especially because low-fitness broodstock may have contributed to previous declines in Cutthroat Trout populations. This study also illustrates that the outcomes of stocking nonnative or native fish species are not always immediately apparent and in some cases might show significant time lags (Crooks 2005). In the North Fork Shoshone River, Rainbow Trout populations did not dramatically increase until decades after their initial stocking. This time lag in the expansion of Rainbow Trout adds complexity to our understanding of the outcomes of fish stocking. Therefore, caution in planning stocking programs, limited stocking of nonnative species, and monitoring the outcomes of stocking, whether for conservation or angling, will be essential to achieving management goals.

CONCLUSIONS

Understanding long-term stocking and survey data is crucial for beginning to untangle the complex forces that shape fish assemblages and can be a useful tool for developing management actions. In this case, historical data provided insight on the status of Yellowstone Cutthroat Trout over the past century that was not apparent when solely looking at current stocking programs and fish population numbers. An understanding of what happened within a system in the past is important for informing current management actions because outcomes of stocking can be extremely variable and prediction is difficult, highlighting the need for continued monitoring following any stocking effort. We emphasize that many aquatic systems have likely been dramatically altered by a long and complex history of fish stocking and that outcomes may not be apparent until many years poststocking.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.