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SPECIAL SECTION: BACK TO THE FUTURE OF RESERVOIR FISHERIES MANAGEMENT—WHAT HAVE WE LEARNED IN 50 YEARS?

Suppression of Invasive Fish in the West: Synthesis and Suggestions for Improvement

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Abstract
Reservoirs are ubiquitous features on the landscape of the western United States. Although reservoirs provide numerous benefits (e.g., irrigation, flood control, hydropower, recreational use), these systems are often a concern from an ecological perspective. Reservoirs support fisheries primarily composed of nonindigenous sport fishes that may become invasive and negatively influence recipient ecosystems. Furthermore, reservoirs alter adjacent riverine habitats, further increasing the threat of invasive fishes to aquatic systems. As such, most western natural resource management agencies focus considerable effort on managing the threat of invasive fish species. Unfortunately, controlling invasive fish is expensive and rarely effective because of a lack of clear objectives, appropriate fishing mortality, and long-term commitment. In an effort to improve management of invasive fish in the western United States, we reviewed existing literature to identify the steps necessary to effectively suppress these species. Specifically, we provide guidance on defining achievable objectives, assessing feasibility, evaluating success, and improving the efficiency of invasive fish suppression. This iterative approach provides managers with a framework to effectively address the challenge of suppressing invasive fish in the western United States.

DEFINITION OF TERMS

Suppression programs are common throughout the western United States and are thus subject to a suite of terms influenced by social, political, and ecological concerns. Although social and political considerations are important, we approach the terminology herein from an ecological perspective to avoid confusion and highlight a science-based approach to suppression programs. As such, we define species that are targeted for suppression as "invasive." The term "invasive" has been used in several ways (Colautti and MacIsaac 2004), but the commonly accepted usage (i.e., a nonindigenous species that is "widespread" and has an adverse effect on recipient habitats; IUCN 1999; McNeely et al. 2001; Gozlan et al. 2010) best reflects the detrimental nature of species that are targeted for suppression efforts. Similarly, the goals of suppression

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programs are subjective and reflect the values of natural resource management agencies and their constituents. Suppression programs may be implemented to conserve native species (e.g., Coggins et al. 2011), benefit species of recreational importance (e.g., Brauer et al. 2019), and (or) improve ecological conditions (e.g., water quality; Bajer et al. 2011). In an effort to avoid value-based terminology, we refer to species assumed to benefit from suppression efforts as "focal species." Although this definition emphasizes populations (rather than ecosystems), in our experience focal species are most often the reason suppression programs are implemented. Finally, various terms have been used to describe "suppression" effort in the literature (e.g., exploitation rate [*u*], total annual mortality [*A*], instantaneous fishing mortality [*F*]). Therefore, any terms herein referring to reductions in population abundance of an invasive species because of management actions will be used synonymously to represent suppression effort.

INTRODUCTION

The ubiquity of reservoirs is no more apparent than in the western United States, where their construction proliferated in the 19th and 20th centuries (Miranda 1996; Graf 1999). Given the vast area they cover, reservoirs in the western United States are highly variable regarding their abiotic and biotic characteristics. For instance, high-elevation western reservoirs exhibit large fluctuations in water level and have relatively short growing seasons, whereas reservoirs at lower elevations are characterized by larger drainage areas, higher total dissolved solids, and longer growing seasons (Miranda 1999). The native fish assemblages of western aquatic systems are fairly depauperate; therefore, reservoirs historically offered little recreational fishery potential. As such, nearly all reservoirs in the western United States have been extensively stocked with a suite of sport fishes (Moyle and Light 1996; Rahel 2000; Kolar et al. 2010). These species provide important recreational opportunities and positively influence local economies. In 2016, nearly 25 million people participated in recreational fisheries in lakes and reservoirs in the United States, contributing to an estimated total expenditure of US\$29.9 billion (where \$1 billion = $\$1 \times 10^9$; USFWS and USBC 2018). Although recreational fisheries are of high social and economic value, the proliferation of species outside their native distribution has important ramifications for the ecology of aquatic ecosystems in the western United States.

Invasive fishes often exhibit deleterious effects on aquatic ecosystems (Britton et al. 2010; Gozlan et al. 2010; Cucherousset and Olden 2011). Invasive piscivores such as Walleye *Sander vitreus* and Smallmouth Bass *Micropterus dolomieu* are now common in the Columbia River basin and are cited as major contributors to the decline of native salmonids (Rieman et al. 1991; Carey et al. 2011). Similarly, invasive salmonids pose a substantial threat to native fish populations and valuable sport fisheries via predation, competition, and hybridization throughout the western United States (Martinez et al. 2009; Hansen et al. 2019b). Introduction of Common Carp *Cyprinus carpio* in the late 19th century resulted in widespread and drastic disruptions to aquatic systems, contributing to the transformation of many systems from clear-water to turbid-water states (Lougheed et al. 1998; Zambrano and Hinojosa 1999; Jackson et al. 2010). As such, the direct effects of invasive fishes are a primary concern for natural resource management agencies.

Unfortunately, western reservoirs not only harbor invasive species but also facilitate the spread of these fish outside of their initial point of introduction. The Smallmouth Bass fishery in the lower John Day River, Oregon, is thought to be the result of an initial stocking of 80 individuals in 1971 (Schrader and Gray 1999). The upstream and downstream movement of invasive fish is a commonly cited threat to numerous native riverine fish populations (McLaughlin et al. 2013; Rahel 2013). Furthermore, reservoirs often create favorable downstream habitats for invasive species, further facilitating their establishment. Altered hydrographs and thermal regimes benefit invasive species in the Colorado River basin, resulting in one of the most extensive suppression programs in North America (Tyus and Saunders 2000; Mueller 2005; Coggins et al. 2011). Altered habitats can also exacerbate the negative effects of invasive species by intensifying species interactions. For instance, reduced water velocity in Columbia River basin reservoirs (e.g., John Day Reservoir, Washington) have intensified predator–prey interactions, resulting in increased consumption of out-migrating Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* (Beamesderfer et al. 1996; Beamesderfer 2000). River reaches with upstream and (or) downstream impoundments exhibited increased catch rates of invasive piscivores and reduced abundance of native cyprinids in the Missouri River basin, Wyoming (Quist et al. 2004). The combined effects of reservoirs have resulted in the proliferation of invasive species, thereby creating substantial concern for nearly every natural resource management agency in the western United States.

Control of established invasive fish populations has been widely discussed in the literature and can be broadly defined as either eradication or suppression (Simberloff 2003; Britton et al. 2010; Gozlan et al. 2010). Eradication is the complete removal of an invasive fish population and is often considered the "gold standard" due to the relative permanency of the action. Unfortunately, eradication is often impractical in complex systems due to the geographic extent of established populations, the cost of treatment (chemical or mechanical removal), and sociopolitical limitations (Meronek et al. 1996; Britton et al. 2010; Rytwinski et al. 2019). Rytwinski et al. (2019)

reviewed existing literature to assess the success rate of mechanical eradication of fish. The authors reported that 42% of the cases reviewed ended in failure and that successful eradications primarily occurred in small, isolated systems. Given that eradication is generally infeasible in large systems, most natural resource agencies pursue suppression programs. The goal of suppression is most often associated with conservation of native species (Mueller 2005; Hansen et al. 2016; Dux et al. 2019); however, suppression programs may also be initiated to benefit recreational fisheries (Hansen et al. 2010; Klein et al. 2016; Klobucar et al. 2016). Regardless, the ultimate goal of any suppression program is to reduce the abundance of the invasive species to limit their effect (e.g., predation, competition, habitat modification, hybridization) on recipient ecosystems (Britton et al. 2010).

The suppression of invasive fish is an inherently long-term management action due to a population's tendency to approach carrying capacity via compensatory mechanisms (Rose et al. 2001). As such, suppression programs represent a significant investment for natural resource management agencies. For instance, reservoir-facilitated increases in piscivory by Northern Pikeminnow *Ptychocheilus oregonensis* on native salmonids resulted in an extensive suppression program in the Columbia and Snake rivers since the early 1990s (Beamesderfer et al. 1996). Since suppression began, about 5 million Northern Pikeminnow have been removed from the Columbia River basin through an angler incentive program that pays between $4 and $8 per fish. Suppression of Lake Trout *Salvelinus namaycush* in Yellowstone Lake, Wyoming, cost nearly $3 million in 2019 (Koel et al. 2020). The initial suppression of mature female Walleye from Buffalo Bill Reservoir, Wyoming, cost between $80 and $491 per individual depending on the gear used (i.e., electrofishing, gillnetting; Kaus 2019). Although the overall cost of suppression programs will depend on various factors (e.g., spatiotemporal extent of suppression, invasive species productivity, stage of invasion), these costs often represent a substantial portion of a natural resource agency's budget and may preclude other important management actions. Therefore, consideration of a suppression program's feasibility is necessary to ensure that limited resources are used wisely. Here, we review existing literature on suppression programs in western freshwater systems and provide guidance on how to approach suppression programs. Specifically, we discuss defining achievable objectives, assessing a program's feasibility, evaluating success, and improving the efficiency of invasive fish suppression in the western United States.

DEFINING OBJECTIVES

Much like other management actions, identifying the objectives of suppression programs is of critical importance. Unfortunately, many suppression programs operate with the vague intent of "removing invasive species" and rarely define clear management objectives (Meronek et al. 1996; Rytwinski et al. 2019; Green and Grosholz 2021). Failure to clearly define objectives is a serious misstep that has ramifications for the planning, implementation, and evaluation of suppression programs (Noble et al. 2007; McMullin and Pert 2010). Well-defined objectives provide managers with explicit, measurable guidance as to what is to be achieved. Once managers define what they are trying to accomplish, a program's implementation, evaluation, and refinement can be more clearly understood (Zale et al. 2012). Thus, one of the first steps in developing effective suppression programs requires defining realistic, quantifiable objectives.

Various approaches have been used to define the objectives of suppression programs. The general goal of most suppression programs is to reduce invasive species abundance below a value hypothesized to minimize their effect on focal species (Britton et al. 2010; Green and Grosholz 2021). In such instances, managers may base suppression objectives on identifiable functional relationships that are assumed to limit the negative effects of the invasive species. Theoretically, linear and nonlinear functional relationships can occur between invasive and focal species (Figure 1). However, the limited research evaluating such relationships suggests that most are characterized by negative exponential decay functions, whereby suppression efforts will have little benefit to focal species (e.g., population increase) until the invasive species is reduced below a specific threshold (Quist and Hubert 2005; Jackson et al. 2010; Weber and Brown 2011; Bradley et al. 2019; Green and Grosholz 2021). Lake Trout in Lake Pend Oreille, Idaho, are managed with the objective of reducing the

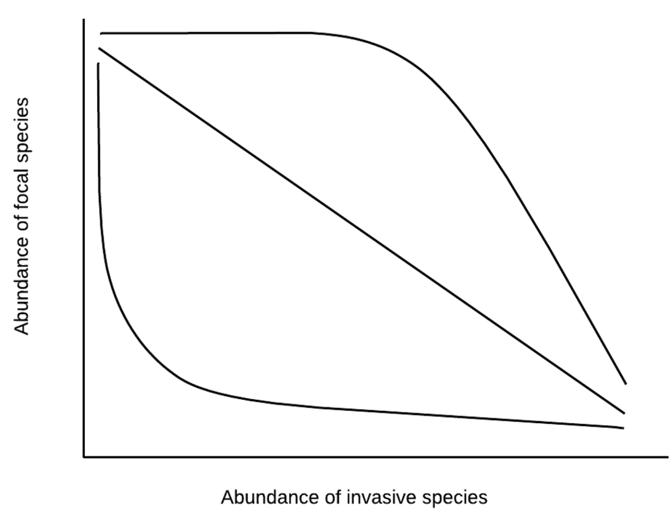

FIGURE 1. Theoretical functional relationships between the abundance of focal species and the abundance of invasive species.

population by 90% of peak abundance (Hansen et al. 2019a). The 90% reduction objective was based on the realization that prior to the exponential increase in Lake Trout abundance, the species exerted relatively little predation pressure on kokanee *O. nerka*. Similarly, threshold relationships were apparent in Iowa and South Dakota where positive effects to sport fish abundance and water quality were not realized until Common Carp were at relatively low densities (e.g., <2 kg/net-night; Jackson et al. 2010; Weber and Brown 2011). Regardless of the actual functional relationship that occurs in a given system, understanding these relationships is critical for formulating realistic expectations and outcomes of suppression programs (e.g., time to achieve desired conditions). For instance, focal species subject to a linear functional relationship may benefit from relatively minor suppression efforts compared to the substantial suppression effort likely required when faced with nonlinear functional relationships. Unfortunately, empirical data on functional relationships are rare. Therefore, managers frequently rely on assumed relationships between focal species and invasive fish populations to define the objectives of suppression programs.

Mortality rates (e.g., instantaneous fishing mortality [*F*]) are often the best metric used when defining the objectives of suppression programs (Figure 2). Because many invasive species are also popular sport fish, existing literature on harvest can be useful for identifying mortality rates that are likely to elicit population declines. The commonly cited 50% annual mortality objective associated with Lake Trout suppression originated from harvest models of Lake Trout in the Great Lakes (Healy 1978). Channel Catfish *Ictalurus punctatus* populations have been found to experience recruitment overfishing once annual mortality exceeds 60% (e.g., Pitlo 1997). When historical estimates are not available, population modeling can be used to predict fishing mortality rates needed to achieve management objectives. One such analysis employs stock–recruitment models to evaluate the relationship between adult abundance and recruitment, thereby defining mortality rates from the population dynamics of the invasive species (Ricker 1954; Beverton and Holt 1957; Maceina and

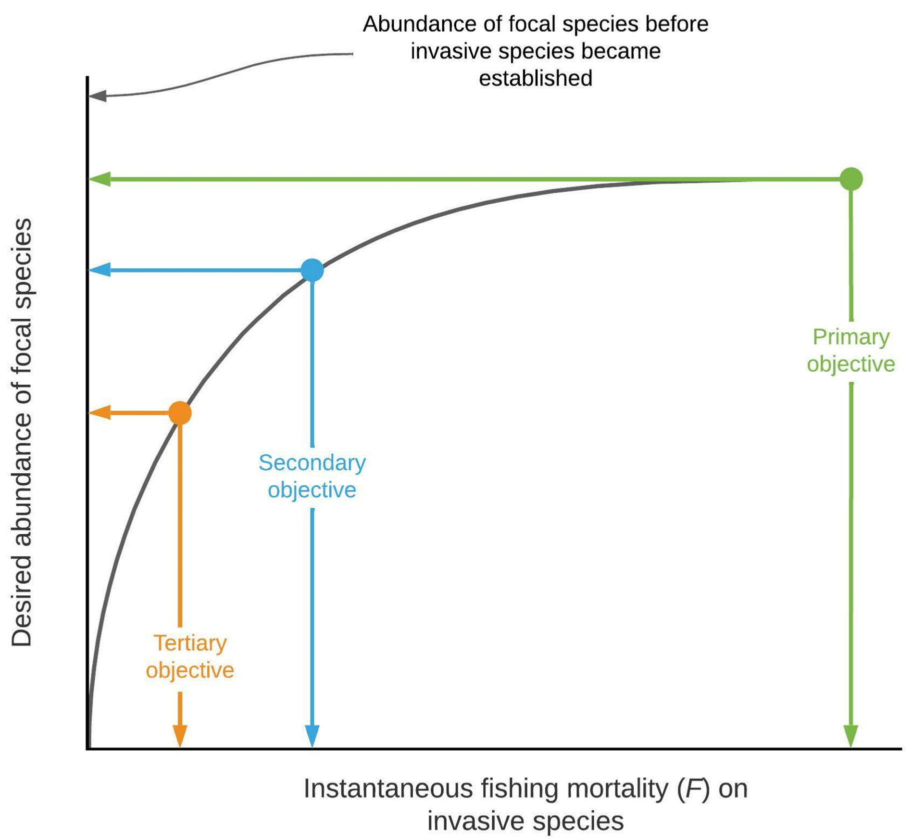

FIGURE 2. Hypothetical relationship between fishing mortality on the invasive species (instantaneous fishing mortality [*F*]) and the desired abundance of the focal species as defined by the suppression program objective(s). Assuming that an invasive species has a negative effect on the focal species (see Figure 1), the abundance of the focal species can never be as high as pre-invasion levels.

Pereira 2007). For example, Beverton–Holt yield-per-recruit models identified that an exploitation rate of 20% would cause recruitment overfishing in invasive Burbot *Lota lota* populations in Fontenelle and Flaming Gorge reservoirs, Wyoming and Utah (Brauer et al. 2018). Similarly, yield-per-recruit models predicted that current levels of fishing mortality of invasive Channel Catfish would not result in recruitment overfishing in the San Juan River, New Mexico and Utah (Pennock et al. 2018).

A similar, yet more flexible, analysis involves the use of stage-structured data (i.e., age or length) to evaluate the influence of fishing mortality on population growth rates (Caswell 2001; Morris and Doak 2002). Specifically, stage-specific estimates of survival, maturity, and fecundity allow managers to understand how suppression scenarios (e.g., changes in fishing mortality rates) influence the growth trajectory of an invasive population. Virtually all of the suppression programs focused on Lake Trout have employed an age-structured modeling approach to guide management of the species (Syslo et al. 2011; Cox et al. 2013; Hansen et al. 2016; Syslo et al. 2020). These analyses predicted that annual fishing mortality rates from 15% to 60% would be necessary to suppress the abundance of invasive Lake Trout in western lakes and reservoirs (Dux et al. 2011; Syslo et al. 2011; Hansen et al. 2016, 2019a). Similarly, Klein et al. (2016) used an age-structured modeling framework to predict that the invasive Burbot population in the Green River, Wyoming, would experience recruitment overfishing once F was equal to 0.43. An added benefit of these types of analysis is that the temporal relationship between suppression and population growth can be evaluated. For instance, Syslo et al. (2020) predicted that Lake Trout abundance in Yellowstone Lake would reach management objectives in 5–20 years depending on annual suppression levels. Stage-structured population models require data that are not commonly collected in monitoring programs (e.g., abundance, survival, fecundity), which may preclude their use. However, population models are vital for successful suppression programs and much of the necessary data can be gleaned from the literature or collected during the initial stages of a suppression program (Caswell 2001; Syslo et al. 2011).

Defining the objectives of suppression efforts can be challenging but is critical for guiding suppression programs and assessing their success (Noble et al. 2007; McMullin and Pert 2010; Zale et al. 2012). Lamentably, identification of project objectives is one of the most overlooked and underappreciated aspects of suppression programs. The desire to remove invasive species is understandable in the face of social and political pressure to conserve focal species. However, it is advisable to avoid initiating suppression programs without clear objectives and an understanding of the fishing mortality needed to reduce the invasive species to levels that achieve the desired conditions. In many instances, the fishing mortality needed to achieve the ideal desired conditions (i.e., primary objective; Figure 2) will be unknown during the initial stages of suppression. However, preliminary suppression effort can focus on "less-desirable" objectives (e.g., secondary and tertiary objectives) while collecting data to better develop realistic, biologically meaningful objectives (Parkes and Panetta 2009; Dux et al. 2019). Without clearly defined objectives, suppression programs will rarely benefit recipient ecosystems, will waste valuable resources, and may diminish the credibility of natural resource management agencies (Parkes and Panetta 2009; McMullin and Pert 2010). For example, after the removal of more than 1.5 million fish in the upper Colorado River basin over 10 years with the expenditure of $4.4 million, native species continued to decline and public support for the program waned (Mueller 2005).

ASSESSING FEASIBILITY

Regardless of the management objectives of a suppression program, the feasibility of controlling invasive fish species should be thoroughly examined given the investment of time and money associated with long-term suppression programs. The feasibility of invasive species control is a complex issue that incorporates social, political, financial, and biological considerations (Parkes and Panetta 2009). A detailed discussion of the socio-political considerations of suppression programs is outside the scope of this paper, but the importance of stakeholder support cannot be overstated (Bomford and O'Brien 1995; Quist and Hubert 2004; Larson et al. 2011). Quite simply, antipathy to suppression efforts will undermine a program's efficacy via factors such as reduced institutional commitment, public disregard for regulations, and litigation (Beamesderfer 2000; Larson et al. 2011; Carey et al. 2012). Financial and biological considerations are inextricably linked, as the time to achieve suppression objectives is directly related to operational costs. Consequently, the likelihood of success from a biological perspective is of paramount concern when planning suppression programs.

Within a biological context, the success of suppression programs hinges on an agency's ability to reduce invasive species abundance below a level hypothesized to achieve the desired conditions. As such, managers must understand the influence of fishing mortality on the abundance of an invasive fish population. In practice, understanding the relationship between fishing mortality and population abundance is often stymied due to limited data on the abundance of an invasive population. Population abundance can be estimated using direct observation (e.g., snorkel surveys, hydroacoustic surveys) or indirect estimation (e.g., mark–recapture methods, removal methods; statistical catch-at-age models; Hayes et al. 2007; Haddon

2011). Given the challenge of direct observation in complex reservoir systems, most suppression studies use mark–recapture or depletion methods to estimate abundance (Syslo et al. 2013; Hansen et al. 2016; Zelasko et al. 2016; Kaus 2019). For instance, mark–recapture surveys were conducted from 2008 to 2014 to estimate Lake Trout abundance in Flathead Lake, Montana (Hansen et al. 2016).

Once abundance is known, the requisite effort (i.e., *F*) needed to reach management objectives can be estimated. Syslo et al. (2013) compared the biological and financial efficiency of suppressing Lake Trout in Swan Lake, Montana. The authors compared various management scenarios that accounted for sampling periodicity, target age-classes, and the associated costs. They concluded that targeting juvenile and adult fish on an annual basis would collapse the Lake Trout population in about 15 years, thereby minimizing overall cost of the suppression program (total cost = $1,578,480). Although the work of Syslo et al. (2013) addressed a suite of objectives, a simpler approach could be used to assess the practicability of any suppression program. Rieman and Beamesderfer (1990) and Beamesderfer et al. (1996) concluded that annual exploitation of Northern Pikeminnow (≥250 mm) would need to be between 10% and 20% (~176,500–353,000 fish) to reduce predation on out-migrating salmon and steelhead by 50%. Despite the value of abundance data for assessing the feasibility of suppression programs, these data appear to be rarely used. Biologists may be hesitant to release fish (e.g., mark–recapture) or conduct additional sampling (e.g., depletion; Hayes et al. 2007). Notwithstanding, the ability to effectively assess the population-level effects of suppression efforts may warrant the short-term cost and effort associated with estimating population abundance.

Even if abundance and fishing mortality information is not available, biological information on the invasive species can be used to understand the general feasibility of a suppression program. Although system-specific dynamics make generalizations difficult (Koel et al. 2020), early maturing, highly fecund species tend to be more difficult to suppress when compared to late-maturing, less-fecund species. Most literature on Lake Trout suppression suggests that populations are susceptible to overexploitation due to the species' slow growth and late maturation (Healy 1978; Martin and Olver 1980; Olver et al. 2004). Simulations suggested that Lake Trout in Flathead Lake would collapse (90% decline) in 11 years once annual mortality reached 45% (Hansen et al. 2016). Recruitment overfishing of Lake Trout was predicted to be achieved in 10 years when annual mortality was 32% in Priest Lake, Idaho (Ng et al. 2016). By comparison, highly fecund species such as Burbot require higher annual mortality rates ($A = 0.57$–0.58) to collapse populations in 10 years (McPhail and Paragamian 2000; Klein et al. 2016; Brauer et al. 2019). Therefore, the higher productivity of certain species will likely require higher levels of annual exploitation or longer periods of suppression to reach management objectives. Despite these generalities, many recipient ecosystems lack the mechanisms that govern fish populations in their native distribution (e.g., predation, competition; Sakai et al. 2001). Therefore, invasive species may exhibit uncharacteristic population dynamics that have the potential to further complicate suppression efforts. For instance, Koel et al. (2020) suggested that survival of pre-recruit Lake Trout was four to six times higher in Yellowstone Lake compared to populations within the species' native distribution. The authors concluded that the absence of embryo predators (e.g., sculpins *Cottus* spp., crayfish *Faxonius* spp.) common in native Lake Trout habitats provided an "ecological release" for pre-recruit Lake Trout in Yellowstone Lake, thereby offsetting Lake Trout suppression efforts. Thus, it is important for managers to understand that suppression efforts (duration and exploitation) are system specific due to complex interactions among invasive fish populations and system characteristics.

System-specific characteristics, such as fish assemblage, population productivity, and physical complexity, may influence suppression efforts. Bycatch of species of conservation concern is a common issue in suppression programs. For example, incidental mortality of Bull Trout *Salvelinus confluentus* as a result of suppression gillnetting for Lake Trout is a concern in systems where both species co-occur (Fredenberg et al. 2017; Dux et al. 2019). In such instances, the costs and benefits of suppression must be considered and may require changes to a suppression program (e.g., reduced effort, changes in techniques; Dux et al. 2019). System productivity can also influence suppression effort due its influence on the abundance of invasive fish populations. Lake Trout in Priest Lake, Idaho, had slower growth rates, poorer condition, and increased rates of skipped spawning when compared to other invasive Lake Trout populations (Ng et al. 2016). The population dynamics of Lake Trout in the system contributed to a relatively low population growth rate ($\lambda = 1.05$) that could be suppressed with less effort ($A = 27\%$) compared to other invasive Lake Trout populations (39–49%; Hansen et al. 2019a). In addition, system complexity and the extent of the invasive population's establishment can influence suppression efficacy. Chemical and mechanical removal techniques are often hindered by complex physical habitat (e.g., sinuosity, cover density; Finlayson et al. 2000; Britton et al. 2010; Rytwinski et al. 2019). Similarly, treating larger geographic areas is inherently more difficult and costly than treating small, less-complex systems (Meronek et al. 1996; Kolar et al. 2010; Rytwinski et al. 2019). Unfortunately, most western reservoirs are physically complex systems that encompass large drainages with variable biological and physiochemical characteristics (Miranda 1999); thus, managers must realistically appraise a program's potential for success given the specific characteristics of a system.

POPULATION MONITORING

Regardless of the selected suppression approach, monitoring is critical for assessing the effectiveness of a suppression program (Figure 3). Much confusion surrounds what constitutes an effective or successful suppression program. Rytwinski et al. (2019) considered a population control method effective if there was quantitative evidence for a reduction in population size (e.g., abundance, biomass, density) or if the reporting authority stated that the invasive fish population was successfully reduced. A similar review considered success to be "changes in standing stock, growth, proportional stock density, relative weight values, catch or harvest, and other benefits, such as angler satisfaction" (Meronek et al. 1996). However, decreased fish density (or associated population metrics) does not necessarily equate to a successful suppression program. Nearly every suppression program removes some number of individuals of the invasive species, but examples of effective suppression programs are rare (Meronek et al. 1996; Rytwinski et al. 2019). As such, the most appropriate gauge of success is fulfillment of objectives as they relate to the desired conditions (Figure 2). Quite simply, if a program's objectives are realized, the program was a success; otherwise, the program needs to be reevaluated (Meronek et al. 1996; Kolar et al. 2010; Rytwinski et al. 2019). In some instances, the objectives of a suppression program will be biologically, logistically, and (or) financially unrealistic. Thus, suppression effort may need to be lowered, the expected benefits to focal species may need to be reconsidered, or the less-desirable decision to end suppression efforts may be required (Figures 2, 3). Moreover, even if objectives have been achieved, managers will still likely need to develop new objectives to ensure that invasive fish populations are maintained at lower densities (Syslo et al. 2013; Dux et al. 2019; Hansen et al. 2019a).

Native fish populations are often the focus of monitoring associated with assessing the success of suppression programs. Propst et al. (2015) concluded that a 6-year removal program was partially successful, as evidenced by increases in the biomass of native species (i.e., Spikedace *Meda fulgida*, Desert Sucker *Catostomus clarkii*) in select reaches of the Gila River, New Mexico. Although monitoring populations of focal species may be valuable for identifying responses to removal efforts, it does not directly assess the efficacy of the removal effort and can result in added time and cost (Brown and Austen 1996; Zale et al. 2012; Rytwinski et al. 2019). A project's success (i.e., achieving objectives) should be assessed directly (i.e., invasive fish population metrics; Brown and Austen 1996) rather than through indirect inference that is subject to numerous confounding factors. For instance, native species recovery nearly always incorporates a diversity of management actions (e.g., habitat restoration, reintroduction), of which invasive species removal is a single component (Beamesderfer 2000; Williams et al. 2011). As such, it is challenging if not impossible to separate the influence of invasive species suppression from the influence of other management actions. Franssen et al. (2014) were unable to determine if long-term removal of Channel Catfish and Common Carp from the San Juan River directly benefited native species recovery because concurrent management actions (i.e., flow manipulations, native fish stocking) also occurred during the 18-year study. Although understanding the ecological ramifications of invasive species removal is important, assessment of an invasive fish population is the only way to directly gauge the efficacy of suppression.

Assuming that the objectives of suppression efforts have been clearly defined, metrics of the invasive population can be used to assess a program's efficacy. For example, population monitoring revealed that Lake Trout suppression in Lake Pend Oreille resulted in a 67% reduction in abundance, which was well below the 90% population reduction goal (Dux et al. 2019; Hansen et al. 2019a). Suppression of Lake Trout in Yellowstone Lake resulted in population declines but did not consistently achieve the program's primary, secondary, or tertiary objectives (Koel et al. 2020). Unfortunately, other examples of suppression program appraisals are concerningly rare. Notwithstanding, assessment of program objectives is the primary means by which efficiency is improved (Dux et al. 2019). Hansen et al. (2019a) identified that targeting juvenile and adult fish in Lake Pend Oreille would result in a 90% reduction in population abundance in 7–13 years. The authors also concluded that once management objectives were achieved, suppression effort could be reduced by about 75%. In addition to direct assessment of a program's efficiency, population monitoring can detect unexpected and potentially problematic responses to suppression efforts.

Fish populations are resilient to natural and anthropogenic perturbations, and they often respond to removal unpredictably. Although population response to removal can be influenced by movement dynamics (Ricker 1954; McMahon and Matter 2006), population stability in the face of suppression is most often associated with compensatory mechanisms (Rose et al. 2001; Zipkin et al. 2009). Compensation is a natural population response to perturbations, whereby reductions in population size are ameliorated through increased growth, survival, or recruitment (Ricker 1975; McFadden 1977; Zipkin et al. 2009). For instance, temporal variations in the population growth

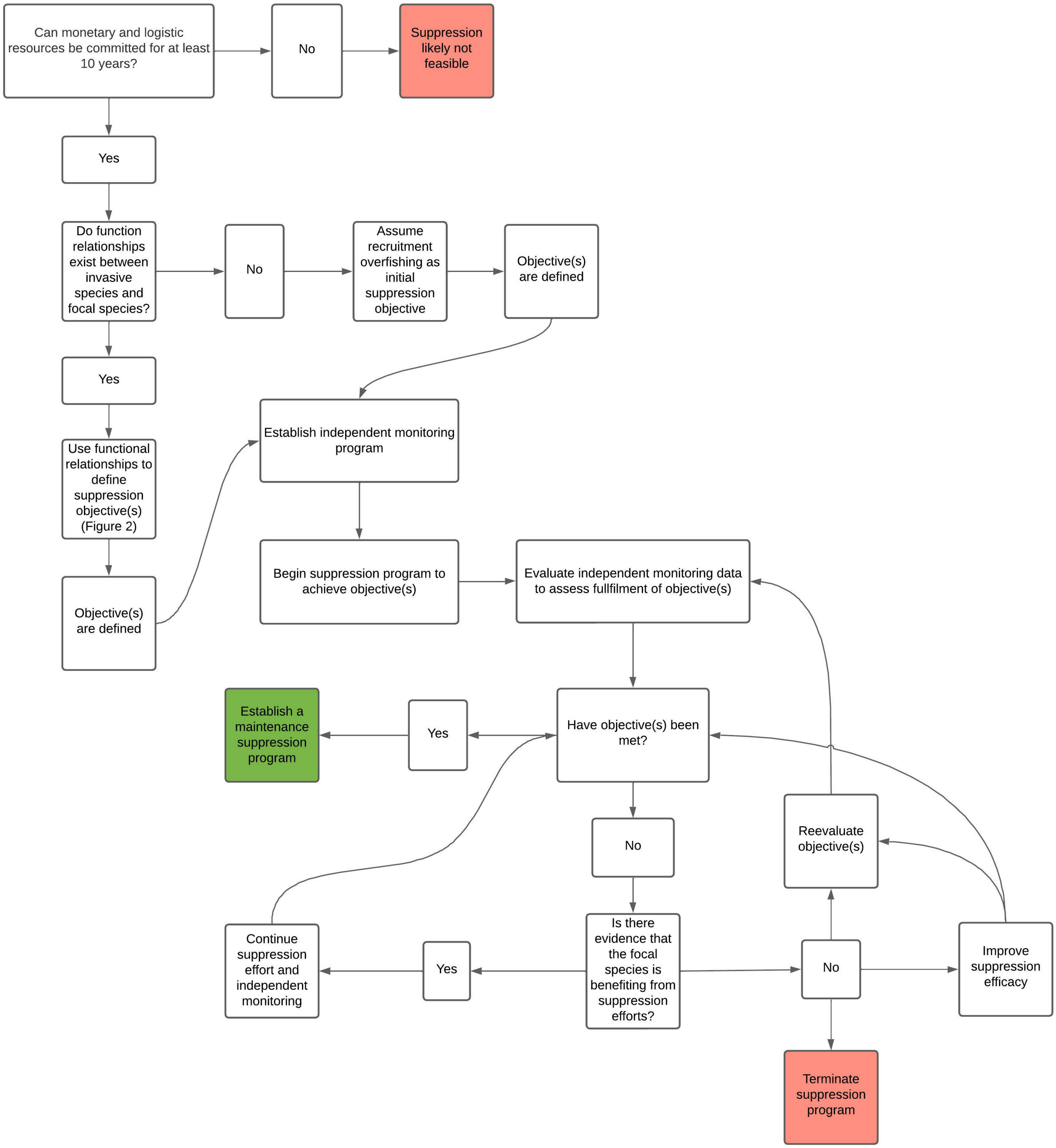

FIGURE 3. Flow chart describing the iterative, science-based approach to suppression of invasive fishes. Red boxes denote "unfavorable" management decisions, whereas the green box identifies the most "favorable" outcome of a suppression program.

rate of Lake Trout were found to be a result of compensatory responses to suppression efforts in Yellowstone Lake (Koel et al. 2020). In certain instances, a population will not only stabilize during suppression but will also overcompensate for losses, resulting in overall population increases (Ricker 1954; De Roos et al. 2007; Zipkin et al.

2009). Despite ongoing suppression from 2004 to 2010, Northern Pike *Esox lucius* abundance annually increased 375–1,000% in three reaches of the Yampa River, Colorado (Zelasko et al. 2016). Similarly, age-0 Brook Trout *Salvelinus fontinalis* abundance increased by 789% after 3 years of mechanical removal in a tributary of the Boise River, Idaho (Meyer et al. 2006). In the context of suppression programs, compensatory responses are obviously problematic. Unfortunately, predicting how a population will respond to suppression is exceptionally challenging; therefore, managers must monitor a population's response to removal to ensure that objectives are being met and to make necessary improvements (Figures 2, 3).

Monitoring success of suppression programs may appear daunting when confronted with the operational costs of suppression efforts, but the importance of monitoring population responses to suppression cannot be overstated (Zale et al. 2012). For instance, much of the success surrounding Lake Trout suppression in Lake Pend Oreille and Yellowstone Lake can be attributed to independent monitoring that allowed for continual reevaluation and revision of these suppression programs (Dux et al. 2019; Koel et al. 2020). Without a clear understanding of the successes and failures of suppression programs, managers are destined to misuse valuable resources and gain little insight on how to improve. However, care should be taken to ensure that monitoring directly addresses the problem at hand to avoid spurious conclusions. In general, clearly defined objectives will greatly enhance managers' ability to identify and evaluate a program's efficiency (McMullin and Pert 2010). Managers can then choose to refine suppression, consider alternative approaches, develop more realistic objectives, or terminate the suppression program (Figure 3).

IMPROVING EFFICIENCY

In many instances, managers will maximize suppression efforts within financial and logistic bounds and still find that they are unable to reach management objectives (Figure 3). Despite over 10 years of intensive (e.g., annual multi-pass electrofishing) removal of Channel Catfish in the San Juan River, little benefit to native fishes was evident (Franssen et al. 2014). Similarly, Saunders et al. (2014) concluded that focused mechanical removal over 2 years was ineffective at reducing Brown Trout *Salmo trutta* densities in a tributary of the Logan River, Utah. In instances where suppression does not achieve management objectives, improving removal efficiency may be the only way to realize success.

Improving suppression efficacy first requires identification of factors contributing to reduced efficiency. Length-structured populations exhibit size-specific patterns in growth, fecundity, and mortality, resulting in disproportionate, length-specific contributions to population growth (Ricker 1975; Caswell 2001). As such, understanding how various length-classes contribute to a population's growth trajectory is necessary for improving efficiency of suppression programs. Using a Beverton–Holt yield model, Feeken et al. (2019) identified that Common Carp in Lake Spokane, Washington, would experience recruitment overfishing at moderate levels of exploitation (0.20–0.40) if 150–450-mm fish were targeted for removal. Targeting 200-mm Channel Catfish in the San Juan River was reported to reduce annual exploitation rates needed to achieve recruitment overfishing from 0.26 to 0.20 (Pennock et al. 2018). When population modeling is combined with sensitivity–elasticity analysis, managers can more clearly identify which stages (i.e., age, length) contribute to population abundance (Caswell 2001). Numerous studies have reported that the population growth rate of Lake Trout is sensitive to changes in the survival rate of age-0 fish (Syslo et al. 2011; Cox et al. 2013; Ng et al. 2016). Sensitivity analysis predicted that a 10% reduction in the survival of age-0 or age-1 Burbot would result in a 40–70% reduction in the population growth rate in the Green River system over 10 years (Klein et al. 2016). In fact, sensitivity–elasticity analysis often identifies the value of suppressing juvenile fish to improve sampling efficiency. However, managers are encouraged to evaluate suppression programs on a case-by-case basis to address system- and species-specific inefficiencies.

Managers often address inefficiencies by targeting alternative length- or age-classes. For instance, increased gillnetting focused on juvenile Lake Trout has greatly enhanced the efficiency of suppression (Syslo et al. 2013; Hansen et al. 2019a). Unfortunately, most gears used in mechanical removal are constrained by inherent size selectivity (i.e., length, girth; Bonar et al. 2009). Klein et al. (2015, 2016) concluded that targeting age-1 and older Burbot would improve suppression efficiency, but the authors noted that age-1 fish only accounted for about 4% of the fish captured over 2 years despite using two sizes of hoop nets (6.4- and 19-mm bar mesh) and night electrofishing. In situations where capture gears are ineffective, managers may employ alternative mechanical removal options. Targeting of seasonal aggregations (e.g., spawning, overwintering) is often suggested to efficiently reduce adult densities (Bajer et al. 2011; Dux et al. 2011; Brauer et al. 2019). Targeting of spawning aggregations via telemetry resulted in a twofold increase in the catch rate of Lake Trout in Yellowstone Lake (Williams et al. 2020). Managers have also suggested targeting rearing habitats to increase mortality of age-0 fish (Thomas et al. 2019; Poole et al. 2020). Lake Trout carcass deposition and subsequent hypoxia resulted in a high average mortality rate (98 ± 1.2%) of Lake Trout embryos in Yellowstone Lake (Thomas et al. 2019). The usefulness of alternative approaches will likely vary by species (e.g., size structure, growth rate) and system (e.g., discharge, depth, productivity), but creative removal strategies may be the only way to improve the success of suppression programs (e.g., Cox et al. 2012).

When changes to mechanical removal options are impractical, managers may consider approaches that can supplement existing suppression efforts. For example, "mandatory kill" policies and liberal harvest regulations are employed throughout the western United States to deter illegal introductions and control invasive fish populations. In the Green, Bear, and Little Snake River drainages of Wyoming, anglers must immediately kill Burbot, Yellow Perch *Perca flavescens*, Walleye, and Northern Pike upon capture (Rahel 2016). Fishery regulation may aid suppression efforts, but these programs rely on catch of fish that may not be routinely targeted by anglers, thereby having little additive effect on fishing mortality rates needed to achieve program objectives (Figure 2). Brauer et al. (2019) reported that exploitation of invasive Burbot in Fontenelle and Flaming Gorge reservoirs likely did not exceed 10%, well below the 20% exploitation rate needed to induce recruitment overfishing in the population. Therefore, anglers in the western United States are often incentivized (e.g., cash, prizes) to increase harvest of invasive fish species (Pasko and Goldberg 2014). Incentivized harvest accounted for 44% of the Lake Trout removed from Lake Pend Oreille over 11 years (Dux et al. 2019). In addition to aiding suppression programs, angler incentive programs involve the public in suppression efforts and may improve public support for control of invasive species (Pasko and Goldberg 2014; Dux et al. 2019). However, incentive programs can be prohibitively expensive and may create unrealistic expectations for stakeholders. For instance, Pasko and Goldberg (2014) warned that the public may become reliant on incomes generated from incentive programs, thereby promoting perpetuation of invasive species via illegal introductions. Nevertheless, angler incentive programs represent a valuable addition to suppression programs, but managers should carefully consider the costs and benefits before implementation of such programs.

An alternative approach for suppressing invasive species involves the use of sex-skewing methods to influence recruitment and long-term population persistence (Gutierrez and Teem 2006; Teem et al. 2014; Schill et al. 2017). The Y-chromosome approach involves introducing feminized fish into wild populations to skew the sex ratio. The original Y-chromosome approach proposed creation of "Fyy" fish (egg-producing fish with two Y chromosomes) using standard aquaculture techniques (i.e., selective breeding, sex reversal; Cotton and Wedekind 2007). Fyy fish can then be stocked into wild populations to mate with wild conspecifics, resulting in all male progeny, 50% of which are "supermales" (sperm-producing males with two Y chromosomes [Myy]; Schill et al. 2017). Although production of Myy fish has proven more tenable due to the technical challenges of producing large numbers of Fyy fish (Teem et al. 2020), the theoretical end result of stocking either Fyy or Myy fish is the eventual collapse of the wild population (Gutierrez and Teem 2006; Teem et al. 2014; Schill et al. 2017). Simulations indicated that low levels of non-selective suppression (10%) combined with stocking of Fyy fish resulted in a 95% probability of extinction of Common Carp in 15 years (McCormick et al. 2021). A hypothetical Brook Trout population was extirpated in 2–4 years when 50% of the wild population was removed annually and replaced with Myy fish (Schill et al. 2017). The Y-chromosome method is a promising advancement in management of invasive species. However, the method remains largely untested in the field (see Kennedy et al. 2018) and may prove particularly challenging in reservoir systems characterized by complex habitats and source–sink dynamics (Brauer et al. 2020). Furthermore, YY broodstock have been developed for only a few common invasive species (e.g., Brook Trout), thus limiting widespread application of the approach.

CONCLUSION

Although success is elusive when confronted with the challenge of controlling invasive fish, many of the more effective programs follow the approach outlined above. These programs identified clear objectives using quantitative methods, developed monitoring programs, evaluated success relative to predetermined objectives, revised objectives and techniques as new data became available, and pragmatically considered expected benefits and outcomes of the suppression program (Fredenberg et al. 2017; Dux et al. 2019; Koel et al. 2020). That is not to say that the approach outlined above will necessarily result in a successful suppression program. However, clear objectives, consistent monitoring, and realistic examination of program success will allow managers to refine suppression programs, thereby enhancing efficiency (Dux et al. 2019). In this manner, managers will be afforded the opportunity to maximize valuable public resources and to be as successful as possible. In many instances, being as "successful as possible" will not translate into biologically meaningful success. When this occurs, managers may need to consider ceasing traditional control tactics for less resource-intensive methods (Beamesderfer 2000).

In light of the challenges of long-term suppression programs, proactive rather than reactive approaches may be the best management option. The benefits of preventing introductions of invasive fish have been widely discussed (Simberloff 2003; Britton et al. 2010; Gozlan et al. 2010); however, controlling the spread of invasive fishes has proven challenging, particularly in systems modified by reservoirs. Many of the most problematic invasive fishes (e.g., Common Carp, Brown Trout, Lake Trout, Brook Trout) in the western United States are the result of historical management decisions (Rahel 2005, 2016; Johnson et al. 2009). Fisheries managers have learned a great deal in the last century, and invasive fish introductions have largely been curtailed or are subject to regulation (Rahel 1997, 2005). Nonetheless, fish introductions continue because of intentional (e.g., illegal sport fish introductions) or unintentional (e.g., aquaculture escapees) releases (Rahel 2005). In western freshwater systems, intentional releases by the public are of particular concern. The proliferation of Burbot in the upper Colorado River basin is believed to be the result of an illegal introduction into Big Sandy Reservoir, Wyoming, in the 1990s (Gardunio et al. 2011). Enforcement to prevent illegal introduction has proven ineffective, but various alternative solutions have been suggested to limit illegal introductions (Johnson et al. 2009). Illegal stocking of Yellow Perch in eight British Columbia lakes resulted in the immediate closure of the fisheries (Maricle 2007). Similarly, the maximum fine for illegally stocking fish in Wyoming was increased from $1,000 to $10,000 in 2010 to better reflect the ecological, social, and economic threats posed by illegal fish introductions (Rahel 2016). To our knowledge, similarly punitive penalties have not been introduced in other states, but the cost of invasive species control may necessitate comparable penalties.

When preventative and traditional control measures prove ineffective, managers may have to institute novel solutions for managing invasive species. Dunham et al. (2020) recently introduced a framework for managing "uncontrollable" species. The managing impact modifier concept focuses on managing the physical and (or) biological factors that influence the effects of invasive species rather than directly controlling the species. The efficacy of the managing impact modifier approach has yet to be tested, but the idea's foundation is supported by previous research. For instance, reestablishment of natural flow and temperature regimes have been suggested as potential mechanisms for reducing invasive species and enhancing native fish recovery (Baltz and Moyle 1993; Stanford et al. 1996; Poff et al. 1997). Short-term restoration of lotic conditions (i.e., reservoir draining) improved out-migration of Chinook Salmon *O. tshawytscha* and reduced resident invasive fish density (Murphy et al. 2019). Similarly, promoting cooler water temperatures via habitat restoration (channel shading) or thermograph alterations (e.g., hypolimnetic releases) may exclude warmwater stenotherms (e.g., Smallmouth Bass; Rubenson and Olden 2017; Dunham et al. 2020). Capitalizing on natural perturbations may also facilitate control of invasive fish. For instance, local extinctions due to high-intensity wildfires may serve as a springboard for invasive species extirpation and reestablishment of native fishes (Armstrong et al. 1994; Rieman and Clayton 1997; Whitney et al. 2015). Although indirect control of invasive species may be difficult to implement in complex systems typical of the western United States, the ever-expanding need to control invasive fish populations may warrant drastic responses.

Like it or not, controlling invasive fish populations is analogous to triage. Invasive fish have entered an ecosystem despite management's best efforts, and drastic action is needed to control the deleterious effects of the invader. Much has been learned about how to effectively approach suppression of invasive species in the last century, but the accumulation of knowledge is useless unless applied appropriately. Managers must consider what they want to achieve and how to get there, and they must follow through by pragmatically evaluating their program (McMullin and Pert 2010). Ideally, this iterative approach will result in an ever-refined approach to controlling invasive species. However, despite best intentions and considerable expenditure of resources, some suppression programs are destined for failure (Meronek et al. 1996; Rytwinski et al. 2019). As such, it is prudent is to be realistic about the feasibility of a suppression program and to thoroughly consider whether a suppression program should be terminated to better focus resources on management actions that will be more beneficial to the species and ecosystems of the western United States.

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