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Bioinvasive species and the preservation of cutthroat trout in the western United States: ecological, social, and economic issues

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Abstract

The cutthroat trout (*Oncorhynchus clarki*) was the only endemic salmonid species across most of the western United States, and it has severely declined largely due to introduction and bioinvasion by non-native salmonid species. However, the ecological, social, and economic consequences of cutthroat trout declines and replacement by non-native salmonid species are relatively minor, and measurable affects on ecosystem function are rare. Restoration efforts for cutthroat trout involve removal or control of bioinvasive salmonid species, but such efforts are costly, ongoing, and resisted frequently by segments of society. Cutthroat trout declines are of little concern to much of the public because they are valued similarly to non-native salmonids, and non-native salmonid species frequently have higher recreational values. Due to the low values placed on cutthroat trout relative to non-native salmonid species, net economic benefits of preserving cutthroat trout are equal to or less than those for non-native salmonids. Cutthroat trout provide a classic case of the consequences of biological invasion; however, other native species are faced with similar issues. We suggest that management agencies establish realistic goals to preserve native species within the context of ecological, social, and economic issues.

Keywords: Non-native; Conservation; Economic; Social; Values; Management strategy

1. Introduction

Human activities have greatly altered natural systems causing measurable and substantial declines in many fish species. Declines of birds and mammals resulting from human-induced disturbances have been documented at global and local scales (Master, 1990, 1991; Richter et al., 1997), and imperilment rates for freshwater fishes, crayfishes, and mollusks have been described as eight times higher than those for terrestrial vertebrates (Master, 1990). Moyle and Leidy (1992) estimated that 20% of the world's freshwater fishes are extinct or in serious decline and over half of the freshwater fishes in the US now receive some form of legal protection in a portion of their range (Johnson, 1987). Most of the federally listed endangered or threatened fish species are concentrated in the western US (Sheldon, 1988). For example, 63% of California's fish species and subspecies are extinct, endangered, or declining (Moyle and Williams, 1990), and nearly all endemic fish species in the Colorado River system have experienced local extirpations and restricted distributions (Mueller and Marsh, 2002; Minckley et al., 2003). Similarly, many native fish species in the Great Plains and Rocky Mountain regions have experienced substantial population and range reductions (Fausch and Bestgen, 1997; McMahon and Gardner, 2001; Behnke, 2002).

Bioinvasive fish species are a significant problem for the preservation of native fishes in the western US. Most non-native fish species were introduced to enhance recreational fisheries, and widespread habitat alterations and continual reintroductions have facilitated the spread of non-native fishes (Gido and Brown, 1999; Mueller and Marsh, 2002). Non-native fish species are regarded as a primary cause for most fish species declines and the most significant limitation to preservation efforts into the future (Sheldon, 1988; Miller et al., 1989; Minckley and Deacon, 1991; Richter et al., 1997; Wilcove et al., 1998; Sala et al., 2000). In the western US, non-native, bioinvasive fish species are considered the leading threat to preservation of native fishes (Minckley and Deacon, 1991; Richter et al., 1997).

Preserving native fishes is dependent on not only understanding ecological systems, but also social and economic issues. We use cutthroat trout (*Oncorhynchus clarki*) to illustrate the ecological, social, and economic issues associated with control of bioinvasive fish species in efforts to preserve native fishes in the western US. Cutthroat trout have declined

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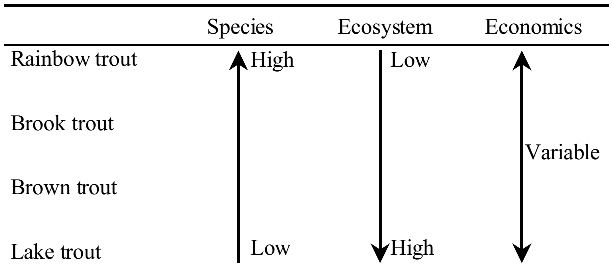

Fig. 1. Conceptual model of the risks associated with preservation of cutthroat trout as a species, risks to ecosystem function, and risks to net economic benefits following invasion by four non-native salmonids. For example, rainbow trout pose the greatest risk to cutthroat trout as a species and the lowest risk to ecosystem function, while lake trout pose the highest risk to the ecosystem and the least risk to cutthroat trout as a species. Economic values are dependent on social values associated with each species and the value of a species is generally independent of its threat to cutthroat trout or their ecosystem.

due to introductions of exotic species and provide a model to illustrate issues facing other native fishes. We contend that arguments for conservation of cutthroat trout should be stronger for this species than for other native fishes of the western US because of their comparatively high social and economic values.

While ecological, social, and economic issues form the basis of our discussion, these issues are presented within the context of a conceptual framework (Fig. 1) that illustrates the positive and negative effects of bioinvasive species. We contend that the relative threats of bioinvasive salmonids may be viewed along two gradients: (1) threats to cutthroat trout as a species and (2) threats to ecosystem function. Additionally, economic effects of bioinvasive species may be positive or negative depending on the comparative social values associated with cutthroat trout or bioinvasive species. Thus, net economic effects of bioinvasion are largely independent of effects on cutthroat trout as a species or ecosystem function. Based on this logic, we evaluate the array of issues facing the preservation of cutthroat trout and other native fishes of the western US. Although our model and discussion focus on cutthroat trout, the arguments may be presented for most native species threatened by bioinvasion.

2. Cutthroat trout

Cutthroat trout had the broadest distribution of any trout species in North America (Behnke, 2002). Behnke (2002) recognized 14 subspecies of cutthroat trout, nearly all of which have been reduced to <5% of their distributions since settlement by Europeans (Kruse et al., 1997; Shepard et al., 1997; Dunham et al., 1999; Horan et al., 2000; Behnke, 2002). Two subspecies of cutthroat trout are extinct, two subspecies are federally listed as threatened, and several subspecies have been petitioned for protection under the Endangered Species Act.

The cutthroat trout is often considered to be a headwater species due to its prevalence in small, high-elevation streams; however, it was historically distributed throughout streams and large river systems (Varley and Gresswell, 1988; Bozek and Hubert, 1992; Dunham et al., 1999; Behnke, 2002). A variety of factors have been associated with cutthroat trout declines (e.g., Liknes and Graham, 1988; Young, 1995; Kershner et al., 1997; Young and Harig, 2001; Campbell et al., 2002), but the most significant influence has been interactions with non-native, bioinvasive fish species (Allendorf and Leary, 1988; Stuber et al., 1988; Kruse et al., 2001; Behnke, 2002). Four non-native species have had the greatest influence on native cutthroat trout: rainbow trout (*O. mykiss*), brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and lake trout (*Salvelinus namaycush*). Behnke (2002) stated that although numerous factors have contributed to the decline of cutthroat trout, “The greatest negative impact, however, has been introductions of non-native trout, especially rainbow trout, with which the cutthroat trout hybridize; but also brown trout, which replace native cutthroat trout in larger streams; brook trout, which have commonly replaced cutthroat trout in small streams; and lake trout, which replace cutthroat trout in large lakes.” The presence of non-native salmonids in most aquatic systems is largely the result of stocking that began in the 19th century (Behnke, 2002). While stocking of non-native salmonids continued throughout the 20th century, stocking has been significantly reduced in recent years. Stocking of non-native salmonids is currently relegated to waters with naturalized populations of non-native salmonids that support recreational angling opportunities. Consequently, the widespread occurrence of non-native salmonids and their effects on cutthroat trout is a legacy of past management practices.

Rainbow trout are a popular sport fish that have been stocked across the western US (Baxter and Stone, 1995; Behnke, 2002), and may pose the greatest threat to survival of native cutthroat trout (Fig. 1). Although rainbow trout compete with cutthroat trout in some systems (Griffith, 1988), their most significant effect is introgressive hybridization (Allendorf and Leary, 1988; Behnke, 2002; Perry et al., 2002). Cutthroat trout generally evolved in allopatry (Behnke, 2002), so a lack of reproductive isolating mechanisms enables introgressive hybridization between cutthroat trout and introduced rainbow trout to occur. The replacement of cutthroat trout by rainbow trout and hybrids throughout a substantial portion of the historic range of cutthroat trout is well documented (Martin et al., 1985; Allendorf and Leary, 1988; Thurow et al., 1988; Henderson et al., 2000; Kruse et al., 2000; Weigel et al., 2003).

Replacement of cutthroat trout by introduced brook trout is widespread and is also a significant threat to cutthroat trout (Fig. 1; Griffith, 1988; Fausch, 1989; Kruse et al., 2000). Brook trout impact cutthroat trout through interference competition (De Staso and Rahel, 1994) and can overwhelm cutthroat trout populations (Griffith, 1988; Behnke, 2002). Age-0 brook trout are typically larger than age-0 cutthroat trout because brook trout spawn in the fall and their young emerge during spring, whereas cutthroat trout spawn in spring or summer and their young do not emerge until summer or early fall, giving the larger age-0 brook trout a competitive advantage (Griffith, 1972, 1988; Behnke, 2002).

Introduced brown trout have replaced cutthroat trout in mid- and low-elevation streams (Bozek and Hubert, 1992). Brown trout have a competitive advantage over cutthroat trout due to their antagonistic, aggressive behavior and fall reproductive strategy (Wang and White, 1994). Additionally, adult brown trout are highly piscivorous and impact survival of cutthroat trout (Behnke, 2002).

Lake trout have been introduced to provide sport fisheries in lakes (Baxter and Stone, 1995; Varley and Schullery, 1998). Adult lake trout are efficient piscivores and can severely reduce native trout populations in lakes where they become naturalized (Cordone and Frantz, 1966; Donald and Alger, 1993; Varley and Schullery, 1998). Because lake trout are a lentic species, their influence is limited to lake ecosystems and pose less of a threat to cutthroat trout populations on a large spatial scale (Fig. 1).

The ecological argument for cutthroat trout preservation is limited if the focus is on ecosystem function. Replacement of cutthroat trout with non-native salmonid species may affect ecosystem function by altering energy and nutrient flow. However, due to their similar ecology, replacement of cutthroat trout with rainbow trout or cutthroat trout × rainbow trout hybrids results in little or no measurable effects to ecosystem function (Fig. 1). The ecology of brook trout is similar to cutthroat trout in stream systems and replacement of cutthroat trout by brook trout likely causes little change in energy flow, nutrient flow, or ecosystem productivity. Thus, rainbow trout, hybrids, and brook trout could be considered ecological equivalents of cutthroat trout in many systems. However, unlike cutthroat trout, rainbow trout, rainbow trout × cutthroat trout hybrids, and brook trout which are insectivores, adult brown trout and lake trout occupy a higher trophic level (Behnke, 2002). Because brown trout are highly piscivorous, they can affect not only cutthroat trout, but also other native fish taxa, such as cyprinids and catostomids (Baxter and Stone, 1995; Fausch and Bestgen, 1997). Changes in fish assemblage structure due to predation by brown trout likely result in alterations to ecosystem function.

Lake trout may pose the greatest threat to lentic ecosystems where cutthroat trout were native (Fig. 1; Varley and Schullery, 1998). In lakes, cutthroat trout are susceptible to terrestrial predators because they often inhabit littoral areas and generally spawn in tributary streams (Varley and Schullery, 1998; Stapp and Hayward, 2002), but lake trout are unavailable to terrestrial predators because they occupy deep-water habitats and spawn in the lake rather than streams. Measurable changes to ecosystem processes are likely to occur where lake trout are introduced (Varley and Schullery, 1998). For instance, in Yellowstone Lake (Yellowstone National Park [YNP]) cutthroat trout have a critical role in linking terrestrial and aquatic ecosystems (Varley and Schullery, 1998). Over two dozen species of mammals and birds utilize cutthroat trout in the Yellowstone Lake drainage (Schullery and Varley, 1995; Varley and Schullery, 1998) and for some species (e.g., osprey [*Pandion haliaetus*], common merganser [*Mergus merganser*], river otter [*Lutra canadensis*]), cutthroat trout are the dominant prey (Varley and Schullery, 1998). Introduced lake trout were discovered in Yellowstone Lake in 1994, where they are expected to alter ecosystem function (Varley and Schullery, 1995; Kaeding et al., 1996; Varley and Schullery, 1998; Reinhart et al., 2001; Stapp and Hayward, 2002; Ruzycki et al., 2003). However, while lake trout pose the greatest overall threat to ecosystem function, they have the least influence on persistence of cutthroat trout as a species.

3. Social issues

The value placed on preservation of native fishes has increased in importance among natural resource professionals, but public support of such activities generally differs from professionals (Muth et al., 1998). Thus, understanding public values related to cutthroat trout and bioinvasive salmonids is critical for obtaining support for preservation activities. Social values can be divided into four major categories: ethical, aesthetic, historical, and recreational.

Ethical values originate from the belief that organisms have intrinsic value and deserve protection from destruction by human activities (Ehrlich and Ehrlich, 1992; Perrings et al., 1992). The notion that species' declines are an indication of changes to overall environmental health and that humans have a moral responsibility to protect the integrity of ecological systems for future generations can be considered an ethical value, and is the view held by most ecologists. With regard to the views of the general public, ethical values may be similar among species. For example, even though non-native trout are removed to protect cutthroat trout, many people are opposed to killing fish for such purposes, regardless of their origin (Stuber et al., 1988; Cailteux et al., 2001).

Aesthetic values are associated with observing the natural beauty of organisms and their habitats (Ehrlich and Ehrlich, 1981, 1992). Viewing cutthroat trout is a popular activity in YNP (Varley and Schullery, 1998); however, observing fish is not a common activity elsewhere. Even if observing fish was a popular activity, many people, including anglers, often cannot differentiate among trout species which are noted for their physical beauty (Varley and Schullery, 1998). Furthermore, replacement of cutthroat trout with non-native trout has no effect on the scenic or aesthetic beauty of the landscape. Thus, there is little evidence to suggest that aesthetic values differ greatly between cutthroat trout and non-native salmonids.

Historical values represent the role of a species in the history of a particular water body, region, or individual. In an historical context, the cutthroat trout was the first trout species recorded by Europeans in North America and was the first trout species encountered by the Lewis and Clark expedition (Trotter and Bisson, 1988). Cutthroat trout also supported a few commercial and subsistence fisheries that helped shape local cultures (e.g., Varley and Schullery, 1998). However, most of society is unaware of the role of cutthroat trout in the history of the western US, suggesting that the historical values of cutthroat trout are either unknown or extremely low. A pertinent concept from social science is "sense of place" (Hall and Page, 1999). Sense of place originates when individuals feel an attachment to a certain place resulting from previous experiences (e.g., previous angling experiences). Non-native salmonid species may be an important component of an individual's sense of place due to historical use patterns, and has lead to opposition of preservation strategies (e.g., Wiley et al., 1993). Throughout most of western North America, replacement of cutthroat trout with non-native salmonids occurred long ago resulting in the development of sport fisheries for non-native species. The contrast between Jackson and Yellowstone lakes in Wyoming is an example of the importance of historical use patterns and sense of place, where lake trout removal may be either resisted (i.e., Jackson Lake; high recreational demand for introduced lake trout) or supported (i.e., Yellowstone Lake; little recreational demand for introduced lake trout) by the public.

The social value with the greatest discrepancy between cutthroat trout and non-native salmonids is probably recreational angling. All five species (i.e., cutthroat trout, rainbow trout, brook trout, brown trout, lake trout) support important recreational fisheries, but replacement of cutthroat trout with non-native species has had either little negative effect or a positive effect on recreational fisheries. Many anglers have no preference among trout species, but cutthroat trout are often considered inferior to other salmonids due to their perceived ease of capture, poor sporting ability (e.g., jumping ability, stamina), and low maximum length (Liknes and Graham, 1988; Campbell et al., 2002). This belief is reflected in angler surveys where there is either little preference among trout species or strong preference for non-native salmonids over cutthroat trout (Reid, 1989; McFarland and Brooks, 1993; McCollum et al., 1999; Gelwicks et al., 2002). Many anglers also fear loss of angling opportunities or implementation of restrictive regulations to protect cutthroat trout populations (Stuber et al., 1988).

Ethical, aesthetic, and historical values are generally not affected by non-native salmonids, and recreational values are likely increased by replacement of cutthroat trout with non-native salmonids. However, exotic salmonid species may be viewed as detrimental in a few areas where the public places a high value on pristine fisheries and ecosystems (Lackey, 2001; Reinhart et al., 2001). Although such views are important for preservation, and will be required to gain public support for restoration activities, few of these places exist outside the national park system.

4. Economic issues

Social issues play an important role in the protection of cutthroat trout from non-native, bioinvasive salmonids and are directly related to economic issues. A common method for assessing the economics of natural resources is a supply and demand model, which illustrates that the price of a resource is based on both its supply and the demand by consumers (Mansfield, 1985; Rees, 1985; Tietenberg, 1996). Although a supply and demand framework may be considered an overly simple model, our purpose is to illustrate patterns among species and to provide a conceptual framework for considering economic issues. Similar models are commonly used in ecological economics as a conceptual framework for assessing economic alternatives and scenarios (Mansfield, 1985; Rees, 1985; Tietenberg, 1996). The demand for a good (e.g., timber, clean water, or cutthroat trout) is depicted by the marginal benefit (MB) curve, which represents the amount consumers are willing to pay down to the last unit of a commodity (Fig. 2A). When the quantity of a good is low,

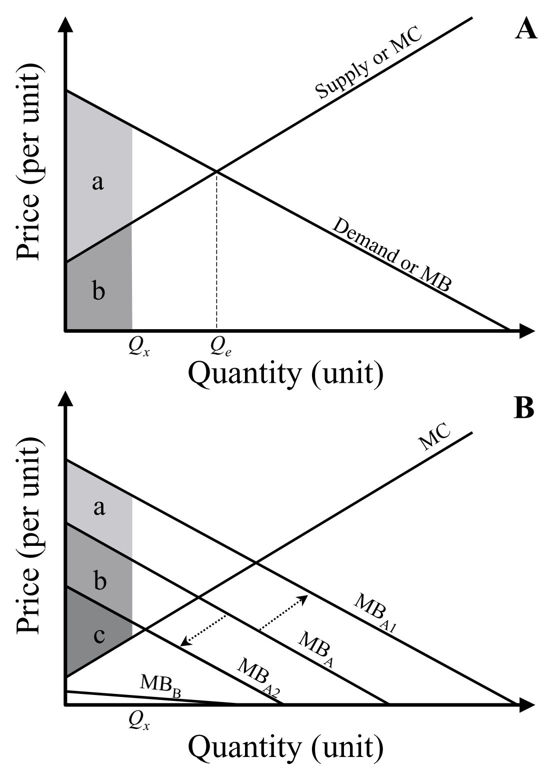

Fig. 2. Conceptual supply and demand model of the benefits and costs associated with a commodity (Panel A). Total benefit of a given quantity of a good is the area under the demand curve, or equivalently, the marginal benefit curve. Total cost is the area under the supply curve, or equivalently the marginal cost curve. The quantity Q_e represents efficient allocation. Panel B represents the marginal cost and marginal benefit for a cutthroat trout fishery. The curve MB_A represents a cutthroat trout fishery in the absence of other species. Bioinvasion can result in an increase (MB_{A1}), decrease (MB_{A2}), or equal demand (MB_{A1}). The curve MB_B represents a cutthroat fishery with little or no demand. Shaded areas in panel B represent net economic benefit of producing trout at quantity Q_x.

consumers are willing to pay a high price, but their willingness to pay decreases for each additional unit of a good. Total benefit, or total willingness to pay (Fig. 2A, area "a + b"), is the area under the curve for any given quantity (Mansfield, 1985; Tietenberg, 1996). The supply curve for a good is depicted by the marginal cost (MC) curve, which represents the additional cost of producing up to the last unit of a good. Total cost is the area under the marginal cost curve for a given quantity (Fig. 2A, area "b"). This model is useful because we can estimate net benefits by combining the marginal benefit and marginal cost curves (i.e., total benefit minus total cost; Fig. 2A, area "a"). We conceptualized the market for cutthroat trout preservation within a supply and demand model. We assumed that marginal benefits would increase as the quantity (e.g., number of individuals, populations, or length of stream with cutthroat trout) decreased and that the marginal cost curve was a positive, linear function of quantity. These assumptions are reasonable within the context of current ecologic and economic theory (Tietenberg, 1996).

Net economic effects associated with bioinvasion of non-native salmonids into a cutthroat trout fishery are contingent on the values society places on each species (Fig. 2B). Thus far, the term "replacement" has been used to describe ecological effects of non-native salmonids on cutthroat trout. In economics, "substitution" reflects a similar concept where an alternative commodity substitutes equally for a commodity that has become depleted or too expensive to purchase or supply (Tietenberg, 1996). Non-native salmonid species may be viewed as ecological and social substitutes in most ecosystems and their bioinvasion has no effect on net benefits of the fishery. For example, if there is a demand for cutthroat trout in the absence of bioinvasive salmonids (represented by MB_A in Fig. 2B), then the net economic benefit of the fishery is area "b + c." When bioinvasion by a substitute species occurs, the net benefit of the fishery is unchanged.

Alternatively, bioinvasion may result in higher or lower net economic benefits depending on social values. If the bioinvasive species is preferred over cutthroat trout, which is usually the situation, demand will shift from MB_A to MB_{A1} in Fig. 2B and net economic benefit (i.e., area "a") will increase. Jackson Lake, Wyoming, provides an example where cutthroat trout were native, but lake trout invaded from upstream lakes that received purposeful introductions (Varley and Schullery, 1998; Stapp and Hayward, 2002). Lake trout now provide the most popular and economically important fishery in Jackson Lake. Similarly, rainbow trout, brook trout, and brown trout are preferred over cutthroat trout throughout most of the western US and their invasion often results in increased economic benefits. In a few systems, net economic benefits may be reduced following bioinvasion. Introduction of lake trout to Yellowstone Lake will decrease demand on the fishery due to the absence of a clientele for lake trout and reduced number of cutthroat trout (Ruzycki et al., 2003). Similarly, when angling for cutthroat trout is a novelty, such as the fishery in Rocky Mountain National Park (RMNP) for federally threatened greenback cutthroat trout (*O. clarki stomias*), bioinvasion of non-native salmonids is likely to reduce demand on cutthroat trout fisheries. Reduced demand on cutthroat trout fisheries would likely have a negative effect on net economic benefits because angling opportunities for non-native salmonids are more readily available outside RMNP. An important point in this discussion is that all scenarios assume that a demand exists for cutthroat trout, but in most ecosystems there is little or no demand (MB_B). With little or no demand for cutthroat trout relative to cost, preservation of cutthroat trout incurs only cost. Moreover, our conceptual model assumes that the cost of producing non-native trout and cutthroat trout is equal. However, producing bioinvasive salmonids requires little cost relative to cutthroat trout suggesting that our models represent a best case economic scenario for cutthroat trout preservation (e.g., MC curve might actually be shifted up for cutthroat trout relative to non-native salmonids).

These simple economic models illustrate the disconnect between bioinvasive species and their effect on cutthroat trout as a species, ecosystem function, and net economic benefits. For example, lake trout have little or no effect on preservation of cutthroat trout as a species, but may have significant impacts to ecosystem function. However, the economic benefits following introduction of lake trout may remain unchanged, increase (e.g., Jackson Lake), or decrease (e.g., Yellowstone Lake) depending on societal values. Bioinvasion by rainbow trout has a significant impact on cutthroat trout as a species, little or no measurable influence on the ecosystem, and varying economic effects. Thus, understanding that risks to cutthroat trout as a species, risks to ecosystem function, and risks to the economic market are independent concepts that must be considered together is critical for developing preservation strategies for cutthroat trout and other native species.

5. Control of bioinvasive salmonids

5.1. Passive approaches

The decline of cutthroat trout has resulted in the widespread adoption of passive approaches to protect remaining cutthroat trout populations. Passive approaches require little or no monetary or labor inputs from management agencies. Passive approaches include changes to harvest regulations or stocking practices, but they have limited effectiveness due to resistance or non-compliance by anglers and the continued spread of naturalized, non-native salmonid species.

Sport fishing regulations have been changed to reduce or prevent further harm to cutthroat trout populations. For instance, cutthroat trout are highly vulnerable to angling and overexploitation (MacPhee, 1966; Liknes and Graham, 1988; Dwyer, 1990; Hepworth et al., 1999), so restrictive harvest regulations have been implemented to protect them, particularly when non-native salmonid species are absent (Gresswell and Varley, 1988; Thurow et al., 1988). Liberal harvest regulations for non-native salmonids may be used to encourage their harvest, but such regulations are often ineffective due to the widespread practice of catch-and-release angling (e.g., Gelwicks et al., 2002). The Idaho Department of Fish and Game (IDFG) liberalized harvest regulations for rainbow trout to protect native cutthroat trout in the South Fork of the Snake River, but because most anglers practice catch-and-release, the regulations have done little to reduce rainbow trout abundance (Henderson et al., 2000; Bill Schraeder, IDFG, personal communication).

The problem of non-native salmonids is a legacy of past stocking practices and although stocking of non-native salmonids has been curtailed in recent times, stocking still occurs in areas with already established populations of non-native salmonids. Thus, changes in stocking practices have been implemented to prevent or reduce effects of non-native salmonid species. If remnant cutthroat trout populations are identified, a strategy to protect populations is to not stock non-native salmonids in the watershed. Because most remnant cutthroat trout populations exist in areas that are remote and inaccessible to the public (Kruse et al., 2001), social resistance to discontinued stocking is generally absent. However, in areas where a fishery has developed based on stocked fish, resistance by anglers can hinder efforts to eliminate stocking programs (Wiley et al., 1993). For example, in Henrys Lake, Idaho, cutthroat trout × rainbow trout hybrids were stocked from 1950 to 1971 to provide a trophy fishery (Campbell et al., 2002). The stocking program was discontinued in 1972 because of concerns regarding introgressive hybridization with native cutthroat trout, but due to the high value (i.e. recreational value) placed on hybrids relative to cutthroat trout, angler groups organized and successfully lobbied the IDFG to reinstate the hybrid stocking program in the mid-1970s.

5.2. *Active approaches*

While passive approaches may slow the spread of non-native salmonids, passive strategies cannot remove established populations of non-native salmonid species that threaten cutthroat trout (Thurow et al., 1997; Dunham et al., 1999). Once an introduced species has become naturalized, their removal is impossible except at small spatial and temporal scales (Thompson and Rahel, 1996). Regardless of the inherent difficulties, active approaches for reducing or preventing interactions between non-native salmonids and cutthroat trout have become an important component of cutthroat trout preservation activities (Stuber et al., 1988; Young, 1995; Ruzycki et al., 2003). Although active approaches are arguably the most effective strategy for preserving cutthroat trout and the ecosystems where they occur, active approaches require ongoing and costly efforts by management agencies. Examples of active approaches include the continual removal of non-native species and construction of barriers to prevent invasion (Novinger and Rahel, 2003).

Reducing the effects of competition and predation on cutthroat trout has been successful in some areas by removing non-native fishes using gears, such as gill nets or electrofishing (e.g., Thompson and Rahel, 1996; Ruzycki et al., 2003). In Yellowstone Lake, an intensive removal effort has been implemented to control introduced lake trout (Stapp and Hayward, 2002; Ruzycki et al., 2003). It has been estimated that lake trout consumed 7% of the annual production of the vulnerable-length cutthroat trout population during 1999, but without control efforts they would have consumed 15% (Ruzycki et al., 2003).

Removal of non-native salmonids may be resisted where a sport fishery has developed. Although cutthroat trout are the only native salmonid in Jackson Lake, lake trout now provide a popular sport fishery in the area. Current management of Jackson Lake focuses on continuing to provide lake trout angling opportunities, so lake trout are stocked annually to supplement natural reproduction. Thus, restoration of cutthroat trout in Jackson Lake in lieu of lake trout is likely to be resisted by anglers.

A common active approach has been the intentional isolation of allopatric populations of cutthroat trout in headwater streams (Stuber et al., 1988; Young, 1995; Kruse et al., 2001; Novinger and Rahel, 2003). This involves the identification of remnant cutthroat trout populations and construction of barriers to prevent upstream movement by non-native salmonids. The objective is to prevent bioinvasion of salmonid species that hybridize, consume, or compete with cutthroat trout (Kruse et al., 2001). Construction of man-made barriers are commonly limited by channel morphology or cost, and they often fail either through lost physical integrity or unsuccessful inhibition of upstream movement by non-native salmonids (Young et al., 1996; Thompson and Rahel, 1998; Harig et al., 2000; Kruse et al., 2001). Furthermore, remnant populations are often in wilderness areas, where construction of barriers may be logistically or legally prohibited (Kershner et al., 1997; Kruse et al., 2001).

Where bioinvasion of exotic salmonids has occurred, fish can be removed using toxicants above a natural or man-made barrier and the stream can be restocked with cutthroat trout. Removing all fish from a stream segment is difficult or impossible due to the presence of springs that dilute toxicants or beaver (*Castor canadensis*) ponds that create unidentifiable channels, even with multi-year treatments (Cailteux et al., 2001; Hepworth et al., 2001). Headwater lakes that contain non-native salmonids are a problem due to logistical constraints (e.g., access) and efficacy of eradication efforts (Stuber et al., 1988). Additionally, anglers have resisted non-native fish removals by reintroducing non-native fish above barriers or into lakes, thereby hindering efforts to re-establish allopatric populations of cutthroat trout (e.g., Stefferud, 1988; Stuber et al., 1988; Thompson and Rahel, 1998; Harig et al., 2000).

Fragmentation and isolation of populations is considered one of the greatest threats to species' survival (Wilcove et al., 1998; Fahrig, 2002), but active approaches to preservation of cutthroat trout populations are guided by a strategy that may jeopardize the long-term persistence of cutthroat trout. While barriers can protect cutthroat trout from invasions by non-native species, protected populations may be too small or have inadequate habitat to enable long-term population viability (Moyle and Sato, 1991; Moyle and Yoshiyama, 1994; Hilderbrand and Kershner, 2000; Harig and Fausch, 2002). Small, isolated populations have high extinction risks due to lost connectivity and gene flow, as well as high susceptibility to stochastic events and demographic variation (Allendorf and Leary, 1988; House, 1995; Dunham et al., 1997; Shepard et al., 1997).

In addition to concerns regarding the efficacy of and resistance to active approaches, a variety of additional ecological issues are important to consider. Treating a stream segment with toxicants not only kills non-native species, but also cutthroat trout, other native fish species, and invertebrates (Kiser et al., 1963; Cailteux et al., 2001). Construction of barriers may have unanticipated effects on other native fishes that depend on habitat in the isolated reach for a portion of their life cycle. For example, a portion of Muddy Creek, Wyoming, is currently scheduled for treatment with toxicants to remove brook trout as part of a cutthroat trout restoration project. However, this same stream segment is inhabited by bluehead sucker (*Catostomus discobolus*), flannelmouth sucker (*C. latipinnis*), and roundtail chub (*Gila robusta*; Michael Bower, US Bureau of Land Management, personal communication), which are all declining native species (Baxter and Stone, 1995). In addition to killing all fish above the barrier, the barrier could have important effects on the population dynamics (e.g., source-sink dynamics) and conservation of other native species.

Active preservation measures are expensive and require continual expenditures. For example, instream barriers constructed as part of projects to restore cutthroat trout commonly cost US$ 100,000–150,000. In addition to the cost of a barrier, other costs such as labor, transportation, fish toxicants, and hatchery production of cutthroat trout for reintroduction could easily be over US$ 20,000/km of stream with a total project cost of several hundred thousand dollars. Furthermore, restoration projects on public lands may require assessments of environmental impacts which may cost over US$ 100,000 for a relatively small restoration project. In Yellowstone Lake, the National Park Service spends over US$ 300,000 annually to reduce lake trout abundance (Varley and Schullery, 1998) and the effort must continue consistently into the future.

It can be argued that species should be saved at all cost and that economic considerations are of no consideration. Regardless of such arguments, reality dictates that preservation activities incur significant costs to management agencies and the public. Because restoration projects are ongoing and costly, obtaining funds for preservation of cutthroat trout is difficult for management agencies. For example, the budget of most state fisheries management agencies is derived almost exclusively from license sales and support from Federal Aid in Sport Fish Restoration, which mandates that agencies focus on sport fishes and limits their ability to conserve non-game species. There is a paradox in this funding structure. For example, the most recent Mission Statement of the WGFDs Fish Division states, "As stewards of Wyoming's aquatic resources, we are committed to the conservation and enhancement of all aquatic wildlife and their habitats...." While state agencies in the western US are committed to conserving all fishes, they have a responsibility to provide anglers with preferred species, which are rarely sensitive native species.

6. Conclusions

Bioinvasive, non-native salmonids have had and are having a significant effect on cutthroat trout. Although brown trout and lake trout are a risk to cutthroat trout populations and ecosystem function in a few areas, the most significant threats to cutthroat trout as a species are rainbow trout and brook trout. Despite these threats, there is little or no social or economic justification for control of rainbow trout or brook trout. Because preservation of cutthroat trout becomes a cost to management agencies with little or no economic benefit, activities to control rainbow trout and brook trout can only be justified based on evolutionary and ecological values. Thus, management agencies must convince the public that preservation activities are the responsible action. Furthermore, agencies must be realistic and realize that only a small number of cutthroat trout populations can be preserved.

Based on this pragmatic view, we recommend a model strategy for cutthroat trout preservation. First, agencies need to initiate collaborations and develop formal management plans with objectives that are measurable, achievable, and acceptable to society and management professionals. The primary goal of management plans should be to preserve a minimum number of secure, sustainable populations within each significant evolutionary unit (i.e. subspecies) of cutthroat trout given the array of ecological, social, economic, and logistical constraints. This goal requires that agencies identify the focal subspecies of cutthroat trout, number of populations to be preserved, minimum viable population size (e.g., 500–5000 sexually mature females), and desired level of genetic purity. Once the management plan has been formalized, current populations need to be surveyed to assess genetic purity of cutthroat trout and to identify populations that are secure, that are threatened by invasion by rainbow trout or brook trout, and watersheds within the natural distribution of cutthroat trout that have suitable habitat but cutthroat trout have been replaced by brook trout, rainbow trout, or rainbow trout × cutthroat trout hybrids. Cutthroat trout populations and their habitats must also be evaluated with respect to their potential for long-term persistence. This evaluation should include the potential size and genetic status of the population, risk of stochastic events (e.g., flood, fire, drought), and potential for geographic dispersal. The magnitude and logistics of initial active preservation efforts also need to be assessed for each site and population. Once cutthroat trout populations have been surveyed and assessed, they need to be ranked and prioritized based on their probability of long-term sustainability and cost of preservation. Cooperative agreements between state, federal, tribal, and private entities, as well as budgets and schedules, must be formalized. As projects are completed, routine monitoring is required to identify maintenance needs and evaluate success. Advances in scientific knowledge and technology, and the success of preservation projects will undoubtedly require agencies to adapt to successfully achieve management objectives. Even though there are many unknowns in this framework (e.g., minimum viable population size, number of populations), a “do nothing” or haphazard approach is not a suitable alternative to a structured approach with formal, well-defined objectives that can be adapted to incorporate new knowledge and changing societal values. Because the cost of preservation is too large a burden for any one management agency and there is a finite number of populations that can be preserved, we must be realistic about our goals and expectations and must rely on cooperation among agencies. The following hypothetical example illustrates these concepts.

Suppose the objective of a management plan is to preserve 20 populations of genetically pure Colorado River cutthroat trout (*O. clarki pleuriticus*), each with at least 1000 sexually mature females, across their native distribution of Wyoming, Colorado, Utah, Arizona, and New Mexico. Our model strategy assumes that there are 100 adult females/km of stream, an average project size involving 15 km of stream, and that the bioinvasive species threat is either brook trout or rainbow trout. An instream barrier costs an average of US$ 150,000 and the cost of treatment (i.e. toxicants), restocking, and associated expenses cost an average of US$ 20,000/km of stream. We assumed a cost of US$ 10,000 per year per project for monitoring following initial restoration efforts. Also, periodic maintenance would be required (i.e. maintenance and rebuilding of structures, treatment of bioinvasive fish above the barrier, restocking of cutthroat trout, and other maintenance costs). We assumed an average maintenance expense of US$ 20,000 per year per project. Therefore, the initial project cost totals US$ 450,000 (i.e. US$ 150,000 for barrier construction + US$ 300,000 for other initial costs [15 km × US$ 20,000/km]) and an annual project cost of US$ 30,000 per year per project (i.e. US$ 10,000 per year for monitoring + US$ 20,000 per year for maintenance). Furthermore, we assumed a commitment to one new project per year until the objective of 20 populations was met and that the rate of annual inflation was fixed at 3%. Based on discussions with agency personnel, these assumptions are reasonable and may actually underestimate costs associated with restoration projects.

During the first year, the only cost (i.e. US$ 450,000) would be the initial cost of constructing the barrier, removing bioinvasive salmonid species, restocking cutthroat trout, and other associated costs. During the second year, the initial cost would be US$ 464,000 (i.e. US$ 450,000 adjusted for inflation) plus the expense of maintaining and monitoring the barrier (i.e. US$ 30,000 × 1 project) constructed in Year 1. In the 10th year, the initial cost for one project would be US$ 587,000 and maintenance and monitoring expenses would be US$ 342,000 resulting in a total cost of US$ 929,000. The costs of monitoring and maintenance become fixed costs, and by year 18, maintenance and monitoring expenses (i.e. US$ 782,000) exceed the initial cost of a project (i.e. US$ 744,000). The final project (i.e. 20th population) would cost US$ 789,000 and monitoring and maintenance of the existing 19 populations would cost US$ 912,000 for a total of US$ 1,701,000 in Year 20. Total cost to preserve 20 populations of Colorado River cutthroat trout would exceed US$ 20,000,000 over the 20-year period. After the goal of 20 populations is established, total costs per year decline because no new projects are instituted. However, the cost of monitoring and maintenance would increase from US$ 98,000 to 1,060,000 per year in the 5 years immediately following establishment of the last population and would continue to increase thereafter.

Many aspects of this exercise could be questioned, including our assumptions of the minimum viable population size and expenses associated with preservation activities. Alternatively, many could argue that 20 populations is too small for the long-term persistence of the subspecies. However, 20 populations is the recovery goal for endangered greenback cutthroat trout (e.g., Young and Harig, 2001) suggesting that our assumptions are reasonable. Regardless of whether our assumptions (i.e. preservation costs, population size) are too large or small, the exercise illustrates that costs to preserve cutthroat trout are real and will represent a significant fixed cost to management agencies. This scenario would insure the persistence of 20 populations of Colorado River cutthroat trout, but if we extend our example across all 11 remaining subspecies of cutthroat trout, it becomes clear that preservation of a minimal number of cutthroat trout populations of each subspecies is a daunting, expensive task.

In an utopian world, cutthroat trout would be highly valued, there would be no financial restrictions, and we could protect or restore all populations, but this is idealistic and unattainable. The issues facing cutthroat trout are shared among other native species. If a solid argument cannot be made for cutthroat trout (i.e. a sport fish species with comparably high economic and social values), what does this mean for other native species facing similar issues? Managers and policymakers must set realistic goals within the constraints of ecological, social, and economic forces. Regardless of whether we want to preserve species, ecosystem function, or both, the reality is that current budgets for preservation activities are limited and only a finite number of populations may be preserved. Determining which populations should be preserved and which should be allowed to disappear is not an enviable task, but reality and logic dictate that choices must be made based on ecology, sociology, and economics. Management agencies need to develop strategies for addressing problems associated with native fish species conservation. The current status of native fish species demonstrates the result of not taking action. A haphazard approach wherein each management agency, jurisdictional region within an agency, or individual has their own agenda is inefficient for long-term preservation goals. Therefore, a formal, collaborative management strategy that can be adapted to new research findings, new technologies, and shifting societal values must be implemented.

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