Rev Fish Biol Fisheries (2015) 25:521–535
DOI 10.1007/s11160-015-9394-x

REVIEWS

Threat evolution: negative feedbacks between management action and species recovery in threatened trout (Salmonidae)

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Received: 20 February 2015 / Accepted: 13 July 2015 / Published online: 22 July 2015

Abstract Resource managers are often presented with dilemmas that require immediate action to avoid species extinction, but that also ensure species long-term persistence. These objectives may conflict with one another, resulting in new threats as initial threats are ameliorated. Such threat evolution is a common pattern in the long history of efforts to conserve endemic trout (Salmonidae) populations in western North America. Early conservation strategies were often successful in reducing initial threats of hybridization with non-native trout, but were also responsible for producing new threats such as inbreeding, genetic drift, and, more generally, reductions in heterozygosity. In such situations, the objective of reducing or minimizing the threat of extinction remains the same, but the causes of decline change in direct response to the implemented strategy. This aspect of species recovery is not often recognized in initial efforts to protect a species from extinction. Here, we present the case of the threatened Little Kern golden trout (*O. mykiss whitei*), as an example of threat evolution. Its conservation management history is well documented, as are feedbacks between direct conservation actions and emerging present-day threats. Management of this and similarly imperiled species must take into account evolving threats, if long-term persistence is to occur.

Keywords Inland trout · Threatened species · Conservation · Threat evolution · Genetics · Fisheries management

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Introduction

Recovery of threatened and endangered species (TES) is a challenging task; many species continue to decline or fail to make progress towards recovery, despite management actions designed to address threats to population persistence. TES status may become a permanent condition if it is an artifact of the late stage of intervention in a species' decline trajectory and of ongoing anthropogenic disruption (Doremus and Pagel 2001). An estimated 84 % of federal Endangered Species Act (ESA)-listed species may be categorized as "conservation reliant," that is, requiring ongoing intervention to prevent extinction (Scott et al. 2010). While the ESA has been successful in preventing extinctions, some have argued that use of available tools under the ESA has yielded only small improvements in species recovery (Gibbs and Currie 2012).

An area of increasing attention in TES recovery planning examines unintended consequences of conservation actions on TES. Numerous examples exist, which we group into three categories: (1) general conservation actions that have deleterious effects on TES, (2) actions that benefit one TES but negatively affect another TES, and (3) threat evolution, where successful measures to enhance a TES lead to deleterious effects of a different nature, on the same TES. Classic examples of the first type occur in biological control efforts (Howarth 1991), where intentional introduction of a non-native species controls a target species, but also negatively impacts a TES species (see Doody et al. 2009; Smith 2005). Other examples within this group include species removals leading to predator or mesopredator release which negatively affects TES (Crooks and Soule 1999); or, where the harvest of an invasive species increases its population growth rate or stability (Zipkin et al. 2009), resulting in an indirect negative effect on a TES. An example of the second type of unintended consequence is the suite of management actions used to stabilize Africa lion populations which have had negative consequences for threatened cheetah populations (Chauvenet et al. 2011). Likewise, Jeffres and Moyle (2012) showed that habitat improvement actions taken to benefit declining Chinook salmon (*O. tshawystcha*) had a negative effect on threatened coho salmon (*O. kisutch*).

The third type, 'threat evolution', occurs when there are unanticipated feedbacks between a particular TES management strategy and that species' response. Specifically, threat evolution transpires when a management action successfully ameliorates an initial threat, but it evolves into a new threat at broader temporal scales (Fig. 1). This aspect of conservation management planning is often neglected because once short-term goals of reducing or reversing declines are achieved, managers often assume an upward trajectory will occur, resulting in a stabilized population. However, if there is insufficient monitoring and a long lag time between management action and a secondary population response, the result can be an unexpected continued decline in the TES.

Here, we review the concept of threat evolution using the case of Little Kern golden trout (*Oncorhynchus mykiss whitei*), an endemic species to the southern Sierra Nevada of California. Initially listed as threatened by the US Fish and Wildlife Service in 1978 (Service 1978), the species has been intensively managed and monitored over nearly four decades. We first discuss the threats that plagued this species preceding its listing in 1978, discuss the management actions used to ameliorate those threats, and then show how those initial threats evolved into new threats in response to management actions. We also review the management history of other declining inland trout species (Salmonidae) and find that threat evolution is common and remains a primary concern for future persistence. Finally, we offer management recommendations for Little Kern golden trout that can be more broadly applied to other similarly imperiled inland salmonids.

Initial threats and management strategy

Native inland fish species decline is occurring throughout North America at an unprecedented rate (Jelks et al. 2008); this is readily apparent in California, where conservation of native fishes has become an onerous task. Of the state's 129 native inland fishes, 83 % are either in severe decline or extinct (Moyle et al. 2011) and 78 % of all California native salmonids are anticipated to be extirpated by 2100 if present trends are allowed to continue (Katz et al. 2013). While the mechanisms of decline vary, hybridization between native and non-native species, especially those from the family Salmonidae, has a long history in California and elsewhere. Declines in native rainbow trout genomes, due to introgression with introduced coastal/hatchery rainbow trout, are increasingly apparent in the phenotypes of trout throughout California and western North America (Cordes et al. 2004, 2006; Finger et al. 2011; Hitt et al. 2003; Kalinowski et al. 2011; Ostberg and Rodriguez 2006; Rubidge and Taylor 2005; Simmons et al.

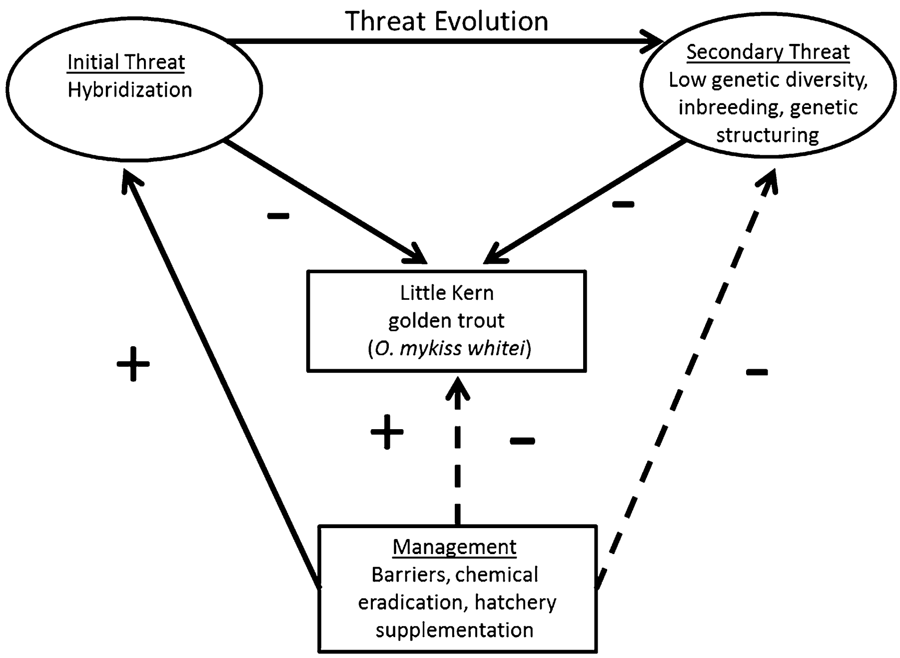

Fig. 1 Conceptual model of threat evolution. *Dotted lines* indicate indirect effects. *Positive sign* indicates a positive effect or the amelioration of initial threat. *Negative sign* indicates a negative effect or the creation of a new threat

2010). Not surprisingly, the conservation of native salmonid genotypes and phenotypes has emerged as a priority of many species conservation programs.

Hybridization has long been a problem for Little Kern golden trout. Even before the species was described in the late nineteenth century, fisheries and over-grazing of meadows had greatly reduced its populations. The principal response of fisheries managers in the early twentieth century was to introduce other species of trout, including coastal rainbow trout (*O. mykiss irideus*), into the Kern River basin to support the fishery (Moyle 2002). By 1975, introductions of coastal rainbow trout had reduced the historical range of Little Kern golden trout by approximately 90 % and fewer than 5000 individuals remained (Christenson 1984; Moyle 2002). The major cause of decline was hybridization, which ultimately resulted in the loss of Little Kern golden trout genes and their distinctive phenotype. Allozyme and meristic studies showed that remaining non-introgressed populations were isolated in five small headwater streams within the drainage (Gall et al. 1976; Moyle 2002).

Due in part to its listing status and in part to its cultural significance as a rare, charismatic sport fish, Little Kern golden trout have been intensively managed over several decades. The lead state agency, the California Department of Fish and Wildlife (CDFW), was tasked with implementing a restoration strategy that would reduce the rate of hybridization between coastal rainbow trout and Little Kern golden trout, while also improving the overall genetic integrity of the endemic fish. A three-tiered management strategy was implemented that consisted of (1) using naturally occurring and constructed fish passage barriers to prohibit non-native dispersal and hybridization between native and introduced species, (2) chemically eradicating non-native and introgressed fish from the basin, and (3) establishing non-introgressed Little Kern golden trout populations, using hatchery-reared fish or wild transplants, in streams from which non-native trout had been removed. Between 1974 and 1996, nearly 100 applications of piscicides were performed on the tributaries, lakes, and main-stem within the Little Kern River drainage, 27 fish barriers were used to isolate populations, and approximately 80,000 fish were transplanted into or within the watershed as part of this management strategy (Table 1). The strategy profoundly shifted the population dynamics and recovery trajectory of Little Kern golden trout.

Using microsatellite DNA loci and single nucleotide polymorphism markers to monitor management progress, Stephens (2007) showed that the three-tiered conservation management strategy was largely

Table 1 Number of chemical treatments, individuals eradicated and restocked (hatchery supplementation), and locations under the initial conservation management strategy order by year

Year	Chemical treatments (N)	Eradication		Hatchery supplementation	
		No of individuals	Location	No of individuals	Source
1974	1	UKN	SL, SC	0	–
1975	2	UNK	BL, LKR	0	–
1979	4	UNK	HL, WMC, TC	0	–
1980	1	31	DC	0	–
1981	4	859	DMC, SSC, LC, LKR	0	–
1982	7	~260	CC, JC, LKR, TC, PC	17	SSC
1983	1	161	RC	0	–
1984	2	102	JC, CC	669	CC,SMC
1985	4	1109+	LC, JC, MC, SSC	1452	FC, LKR, JC, MC, BL, ML
1986	2	UKN	MC, CC	991	SMC, JC, CC, LKR, BL, FC
1987	2	159	SC, CC	0	–
1988	5	704	RC, SC, PC, CC, TMC, LKR	2590	CC, BFL, LKR
1989	5	473	SL, SC, SSC, CC, PC, TMC	10,993	BFL, CC, JC, LKR, SSC, SMC, TMC
1990	3	10,501	ML, AMC, LKR	1963	ML, PCC, TL
1991	8	UNK	AC, PCC, MC, TL, RL/C, FL/C, TWL, PCC	5128	AC, ML, PCC, TL, BL
1992	6	2775	PCC, MC, FC, CC	5328	PCC, ML, TL
1993	7	948+	PCC, TWL, ML, MC, LKR, CC, WC, TC	0	–
1994	10	1479+	PCC, AC, CC, MC, GMC, LKR, LC, FC	20,358	PCC, ML, TL, LKR, SSC, AC, MC, SSC
1995	4	11	TMC, JS, UNCs	12,549	MC, AC, SSC, TWL, ML, LKR
1996	4	90	RC, BL, LKR, TWL, MC, AC, ML	8868	LKR, TWL, MC, AC, ML
1997	0	0	–	10,029	CC, LKR, TL ML
Total	82	19,662+	–	80,935	–

Specific locations are abbreviated and are as follows: *SL* Silver Lake, *SC* Shotgun Creek, *BL* Bull Frog L, *LKR* Little Kern River, *HL* Hidden L, *WMC* Wet Meadow C, *TC* Tamarack C, *DC* Deep C, *DMC* Deadman C, *SSC* Soda Spring C, *LC* Lion C, *CC* Clicks C, *JC* Jacobsen C, *TC* Table Meadows C, *PC* Pistol C, *RC* Rifle C, *MC* Mountaineer C, *TMC* Trout Meadow C, *ML* Maggie L, *AMC* Alpine Meadow C, *PCC* Pecks Canyon C, *MC* Maggie C, *TL* Tadpole L, *RL/C* Rosie Lake/Creek, *FL/C* Frog Lake/Creek, *TWL* Twin L, *FC* Fish C, *WC* Willow C, *GMC* Grey Meadow C, *JS* Jugs Spring, *UNCs* Unnamed C, *SMC* South Mountaineer C, *UKN* unknown

successful at removing the genetic influence of coastal rainbow trout on Little Kern golden trout. While a few isolated populations continued to exhibit moderate levels of introgression, post-strategy monitoring showed that 85 % of Little Kern golden trout populations contained <5 % rainbow trout introgression (Stephens 2007). The conservation actions used to reduce the influence of the coastal rainbow trout, however, were not without consequences. After nearly 30 years of implementing the three-tiered strategy, evidence of negative feedbacks between the strategy and genetics of Little Kern golden trout became apparent.

Considerable genetic structuring now exists among populations that corresponds with the reintroduction history of hatchery-reared Little Kern golden trout following the eradication of hybridized populations (Stephens 2007). Populations are typified by high F_{ST} values, significant F_{IS} (inbreeding) coefficients, evidence of genetic bottlenecks, and relatively low heterozygostity and allelic richness values (Table 2). These findings were likely a result of a combination of factors associated with both the management history of the basin and the conservation management and reintroduction strategy. Low levels of genetic heterogeneity may at least partially be an artifact of a

Table 2 Summary of genetic results presented as the range of population averages within each group, including hatchery broodstock samples (BS), populations within the native range (NR), out-of-basin transplants (OBT), and hatchery and wild rainbow trout (RT) reference populations (Ref)

Population ID	qRT (msat) (%)	qRT (nSNP) (%)	Bottlenecked	N	H_E	H_o	Na	r	F_{IS}	F_{ST}
LKGT BS	0–4	1–5	1/3	8–38	.49–.66	.46–.64	3.8–5.8	2.5–3.0	.02–.22	.19
LKGT NR	0–10	1–34	13/16	10–39	.34–.65	.28–.61	2.3–6.4	1.9–3.3	−.05 to.18	.29
OBT	92	2–18	0/1	28	.75	.65	9.9	4.4	.14	n/a
RT Ref	96–99	94–98	0/4	18–30	.73–.8	.67–.76	6.3–9.9	3.9–4.9	.01–.14	.15

Average percent-wide rainbow trout admixture (qRT) is given for each group for microsatellite (msat) and nuclear SNP (nSNP) data. "Bottlenecked" refers to the number of bottlenecked populations observed out of the total populations examined in each group (where minimum $N = 20$), while "N" give the range of population sample sizes. Number of alleles (Na), rarefied allelic richness (r), observed and expected heterozygosities (H_o and H_e), estimates of inbreeding (F_{IS}), and population subdivision (F_{ST}) are also provided

historically limited gene pool associated with few remaining populations preceding federal listing in 1978. The usage of barriers to segregate reintroduced populations and a restocking regimen disproportionally focused on the use of hatchery-reared individuals with low genetic diversity also likely contributed to reduced genetic diversity range-wide.

Short-term benefits and long-term consequences

Fish passage barriers

Stream barriers discouraging fish passage have been shown to negatively affect life history, population dynamics, genetics, and ecology of wild salmonid populations. While the short-term benefits of population isolation have proven effective in reducing the incidence of hybridization, and the potential for loss of native genotypes, competition, and predator–prey interactions between native and non-native fishes, there are also several long term consequences associated with these structures (Hilderbrand and Kershner 2000; Novinger and Rahel 2003). Fish barriers limit dispersal to more favorable habitats during unfavorable conditions and may increase the possibility of population bottlenecks (Hilderbrand and Kershner 2000; Kruse et al. 2000; Morita and Yamamoto 2002). Barriers also reduce the ability of native fishes to migrate to spawning, rearing, and over-wintering and summering habitat and may adversely affect demographic structure and population dynamics (Auer 1996; Neraas and Spruell 2001; Sheer and Steel 2006). These effects may be compounded by overall reductions in gene flow, loss of heterozygosity through genetic drift, and increases in intraspecific competition (Wofford et al. 2005). Wofford et al. (2005) found that barriers intensified genetic structuring and loss of allelic richness due to genetic drift in coastal cutthroat trout populations. Hilderbrand and Kershner (2000) suggested that long term persistence of inland cutthroat trout may be compromised by reductions in effective population size due to a lack of habitat continuity and complexity associated with fish passage barriers. Likewise, Deiner et al. (2007) found that rainbow trout populations above barriers were highly structured and showed lower levels of genetic diversity when compared with below-barrier populations in continuous reaches. Irrespective of the historical mechanisms contributing to the findings of Stephens (2007), dispersal barriers once used effectively in the initial management strategy for Little Kern golden trout have likely contributed to reductions in gene flow and intensified inbreeding within and genetic differentiation among Little Kern golden trout populations.

Chemical fish removal and restocking

Additional components of the Little Kern golden trout conservation management strategy included eradication of introgressed populations with piscicides followed by relocation of wild fish from known source populations within the basin, stocking of hatchery-reared Little Kern golden trout, or a combination of both. While the strategy initially focused on relocating wild fish to encourage outcrossing and improve genetic diversity, resource managers became increasingly dependent on captive bred Little Kern golden trout through time (Fig. 2). Of the approximately 80,000 individuals that were transplanted in the Little Kern basin between the time of listing (1978) and

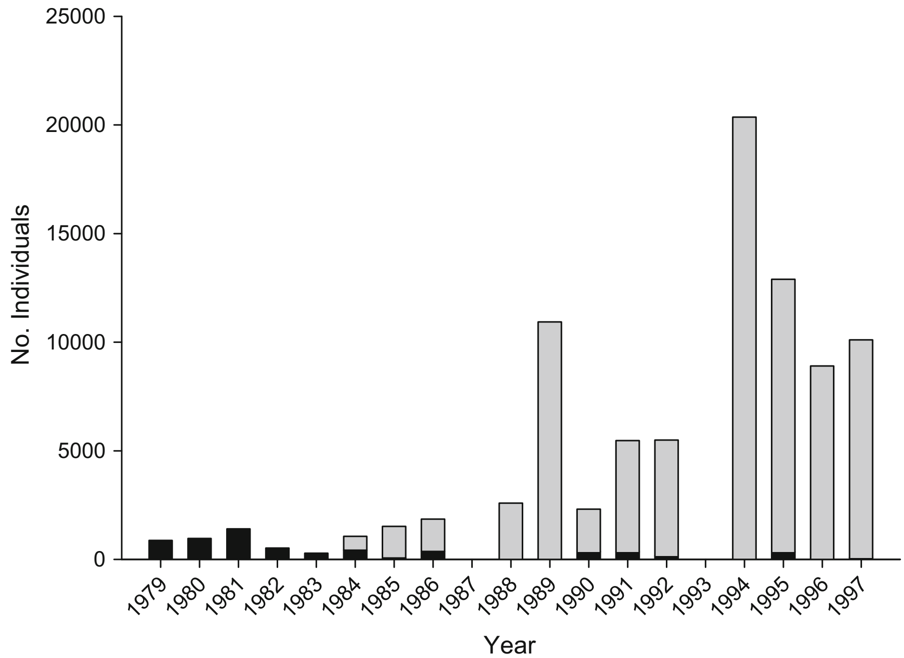

Fig. 2 Number of translocated wild Little Kern golden trout (*black bars*) and hatchery reared Little Kern golden trout stocked (*grey bars*) in the Little Kern River drainage between 1979 and 1997

when restocking ceased (1997), 93 % were of hatchery origin. Similar to dispersal barriers, captive breeding of salmonids has also been shown to have numerous population consequences for wild individuals (Fraser 2008).

Eradication of fish populations for restorative purposes usually precedes a program of reintroduction. This strategy has been used with many inland salmonid populations, including Little Kern golden trout. Reintroduced individuals are often produced by captive breeding programs where parental phenotypic traits (size, color, etc.) may be selected by managers. Progeny are reared in captivity and eventually released into the wild. Conservation hatcheries typically follow more stringent mating protocols in order to preserve ancestral lineages or ecologically divergent populations (see O'Reilly and Kozfkay 2014; Wares et al. 2004). While historically rare, this practice has recently become more common (Maynard and Trial 2014). Depending on selection intensity, parental genetic diversity, number of generations reared in the hatchery environment, and effective population size, many captive bred species may become genetically adapted to the hatchery environment with long term population costs for both wild and natural origin populations (Chilcote et al. 2011; Frankham 2008; Ryman and Laikre 1991). Parental genetic diversity associated with the Little Kern golden trout captive breeding program was often limited due to low effective population sizes. In addition, second and third generation hatchery offspring were used at times as broodstock to establish wild populations (C. McGuire, CDFW, personal communication).

Hatchery-reared salmonids typically show a decline in fitness in the wild and overall reductions in genetic heterogeneity (Allendorf and Phelps 1980; Araki et al. 2007; Ford 2002; Heath et al. 2003). This stems from selection for maladaptive traits in the hatchery environment, limited parental genetics, inbreeding depression, or a combination of these factors. For instance, Christie et al. (2012a) showed that first generation hatchery-reared salmonids increased their reproductive output in captivity by two-fold when compared with their wild siblings, indicating selection of hatchery specific traits that may be otherwise deleterious in the wild. Chilcote et al. (2011) showed that interactions between hatchery and wild species precipitated strong declines in reproductive performance of natural origin salmonids, and further, demonstrated that this result occurred irrespective of the source of the hatchery broodstock (i.e., domesticated vs. wild). Others have shown that hatchery-reared individuals can reduce effective population size of wild populations and cause artificial increases in population density that produce strong density dependent effects (Christie et al. 2012b; Kostow and Zhou 2006).

In consideration of the vast literature on hatchery-reared salmonids and their effects on wild populations, we suggest the use of hatchery fish for restoration also had long term consequences for Little Kern golden trout. Recent observations of low genetic diversity are partially an artifact of the extensive use of hatchery-reared individuals in the basin. Consequently, extant populations may lack sufficient genetic diversity to adapt to changing environmental conditions, suffer from hatchery-induced fitness reductions, and negatively affect fitness of remnant wild fish.

Management recommendations

Implementation of the Little Kern golden trout conservation strategy largely eliminated the initial threat of hybridization with introduced coastal rainbow trout, but at the same time, produced new threats. The mechanisms of genetic decline differ between initial listing and post strategy implementation, but threats to persistence remain. In order to ensure the recovery and long term persistence of Little Kern golden trout and other inland salmonids, changes to conservation management strategies are required. To improve the current genetic status of Little Kern golden trout, we recommend (1) genetic monitoring to fully delineate the spatial extent of all populations and monitor rainbow trout introgression within the drainage, (2) relying less on hatchery-reared individuals to restore the population to its historical range or ensuring that conservation hatchery methods are strictly employed, (3) using fish passage barriers more strategically to limit gene flow where threats are greatest and at headwater reaches in order to protect differentiated stocks and to reduce the number of redundant barriers, and (4) establishing additional refuge populations outside the drainage to buffer against the potential for future population reductions within the drainage. We believe that these management prescriptions can be more broadly applied to other inland salmonids with similar ecology, life history, threat, and management profiles.

Genetic monitoring

While the current genetic landscape of Little Kern golden trout populations within the drainage has been mostly characterized (Stephens 2007; Stephens and May 2010), it is important to ensure that all tributaries and perennial streams within the native range are analyzed. This will identify remaining moderately to highly introgressed populations and provide important insight on the spatial proximity of 'pure' and introgressed populations. While introgressed populations may be subjected to additional eradication efforts, non-introgressed populations should be the focus of reestablishing connectivity between populations. We suggest that this should initially be approached cautiously and at an experimental level in order to first understand how increases in population connectivity affects effective population sizes, heterozygosity, and, ultimately, fitness. Additionally, connectivity should only be facilitated between populations with similar ancestry (see Stephens et al. 2013). Full genetic spatial delineation of the drainage will aid in minimizing the risks associated with experimental introductions, while maximizing benefits of an adaptive conservation strategy.

Management of genetically structured populations

Currently, populations of Little Kern golden trout show low levels of genetic diversity and significant genetic structure between populations. These outcomes are at least partially a result of disruptions to gene flow initiated by dispersal barriers and 50 years of systematic reintroductions of hatchery-reared individuals. The current genetically structured populations may in fact offer an opportunity to increase effective population size and reduce inbreeding at the species level, while also maintaining structured populations in the wild where differentiation through genetic drift is encouraged. Margan et al. (1998) showed that maintaining several captive distinct small populations with occasional translocation of individuals between populations resulted in similar or improved genetic diversity and evolutionary potential when compared to one large population and others have come to similar conclusions (Frankham 2008). We suggest an analogous strategy for Little Kern golden trout in which genetically structured populations are maintained in headwater reaches and isolated by preexisting barriers, while larger and more genetically diverse populations are maintained below these reaches. Imperative to this strategy is the selection of continuous headwater reaches exhibiting a range of habitat features. Genetically ‘pure’ and differentiated individuals from headwaters should occasionally be relocated to other stream segments so that exchange of genetic material between populations can increase effective population size in currently fragmented tributary populations, reduce inbreeding, and improve heterozygosity. Huff et al. (2010) showed that mixing genetically divergent populations of slimy sculpin (*Cottus cognatus*) improved allelic richness and genetic diversity when compared with individual genetic sources used during reintroductions; they suggested that the strategy was most appropriate for small isolated populations experiencing declines in heterozygosity from inbreeding depression. Such a source mixing strategy may also encourage the removal of rainbow trout alleles in minimally introgressed populations (i.e., <1 %) through genetic swamping. However, such efforts may be impeded if rainbow trout alleles retain a selective advantage in the wild. While we believe the possibility to be unlikely, such a genetic rescue effect strategy should be applied cautiously and in a step-wise manner to ensure that crossing differentiated individuals does not cause a reduction in population fitness via outbreeding depression (Tallmon et al. 2004).

There are additional benefits to using headwater reaches, rather than mid- or lower-order reaches, to isolate genetic stocks. First, headwater reaches are often difficult to access which reduces potential for purposeful reintroduction of rainbow trout or introgressed individuals. Indeed, after 50 years of systematic rainbow trout introductions to the basin, remnant Little Kern golden trout populations existed only in five headwater reaches before their federal listing in 1978 (Gall et al. 1976; Moyle 2002). Second, many fish barriers in the Little Kern drainage are natural barriers (i.e., cascades or waterfalls). Maintaining individual stocks in headwater reaches greatly reduces the threat of downstream emigration of introgressed individuals and stock contamination. Finally, headwater reaches may act as important genetic strongholds for Little Kern golden trout and similar species. Numerous cutthroat trout populations have experienced drastic declines in their distribution and headwater reaches often serve as critical refuges for remnant ‘pure populations’ (see Behnke 2002). Kruse et al. (2000) suggested that Yellowstone cutthroat trout (*O. clarkii bouvieri*), a similarly imperiled inland salmonid, retained a physiological advantage in headwater reaches, making them more resilient to negative interactions with introduced species (Bozek and Hubert 1992; Kruse et al. 2000). In short, implementing a strategy that focuses on both maintaining genetically differentiated stocks and outcrossing individuals through relocations will maintain genetic differentiation at the individual level and vastly improve genetic diversity at the species level (Frankham 2008).

Relying on naturally reproducing populations to improve genetic diversity has many additional benefits when compared to a strategy of reintroducing hatchery-reared progeny. There are of course circumstances where captive breeding must be an integral part of species recovery, especially for species that are critically endangered. In less severe cases, however, benefits of augmenting populations with hatchery-reared individuals are not fully understood (Fraser 2008). Recent research suggests that using captive breeding for wild population augmentation may lead to a loss of important genetic adaptations, life history traits, and reduced fitness (Christie et al. 2012a; Heath et al. 2003; Neff et al. 2011; Petersson et al. 1996). For Little Kern golden trout, a strategy that incorporates the natural environment, wild progeny, and outcrossing between populations to improve heterozygosity may be warranted. Such a strategy could ameliorate current genetic deficiencies while ensuring that critical genetic adaptations and life history traits are maintained, potential reductions in wild-type fitness from interactions with hatchery-reared fish are diminished, and genetic heterogeneity of the species is greatly improved.

Finally, maintaining genetically structured populations and redundant genotypes in the wild also reduces species vulnerability to stochastic events such as wild fires, floods, drought, tectonic or volcanic activity, and disease. For instance, during the summer of 2011, the Lion Fire burned over 20,000 acres and up to 97 % of upland habitat immediately adjacent to numerous tributaries containing Little Kern golden trout (Teater 2011). While effects of the fire on Little Kern golden trout are not yet fully understood, studies have shown that forest fires can vastly change watershed processes and cause fish mortality (Bozek and Young 1994; Earl and Blinn 2003). Loss of particular populations during these types of events could be effectively buffered against with maintenance and reintroductions of genetically differentiated source populations.

Strategic use of fish barriers

In some cases it may be appropriate to remove or alter fish passage barriers within the drainage to promote connectivity. Several studies have shown a positive correlation between available habitat size and genetic diversity (Honnay and Jacquemyn 2007; Neville et al. 2009). Using a Bayesian network model, Peterson et al. (2008) found that westslope cutthroat (*O. clarkii lewisi*) populations were less resistant to brook trout (*Salvelinus fontinalis*) invasions when they were isolated into fragmented populations by barriers. Their analysis suggested that habitat heterogeneity and connections between populations retained westslope cutthroat trout life history characteristics and effectively diminished the competitive influence of brook trout. Similar to Little Kern golden trout, cutthroat trout are also extremely susceptible to hybridization with rainbow trout and although the authors did not directly model the potential risks and benefits of barrier removal with respect to rainbow trout and the potential for introgression, they suggested their analysis may be informative for such circumstances. From a genetic perspective, removing or altering selected barriers will promote gene flow between populations of Little Kern golden trout, reduce inbreeding, increase effective population sizes, and improve genetic heterogeneity. The benefits of such a change in management strategy, however, are not strictly genetically based. Promoting greater instream connectivity can also enable populations to retain key life history characteristics, access critical seasonal habitats, improve population demography, evade high mortality events associated with environmental stochasticity, and provide a recolonization mechanism for stream reaches that recently experienced such events (Kozfkay et al. 2011; Kruse et al. 2000; Neville et al. 2009).

The benefits of instream connectivity are particularly germane in consideration of a changing climate. Changes in the timing and magnitude of stream flow are anticipated in California, with models indicating that runoff will occur earlier in the spring, and, thus, extend the annual baseflow period during the summer and early fall (Miller et al. 2003). Prolonged low flow periods are associated with high thermal stress to cold water fishes and overall reductions in habitat availability. This suggests that cold springs and pools will become increasingly important as thermal refuge areas, especially during periods of drought as recently experienced in California. Increased connectivity will provide access to these habitats and others such as overwintering, spawning, and rearing areas while also reducing intraspecific competition (Novinger and Rahel 2003). Barrier removal and increased connectivity would also likely reduce population consequences associated with mortality-inducing events such as wildfires, which are anticipated to increase in frequency with climate change (Westerling et al. 2006), by providing greater dispersal potential to refuge habitats.

There are significant risks associated with a strategy of barrier removal. Reconnection of fragmented populations may enable introgressed individuals or reintroduced rainbow trout to hybridize with Little Kern golden trout populations. In order to minimize potential risks and maximize the genetic, demographic, and ecological benefits of barrier removal, prioritizing populations for reconnection should be based on genetic structure. Ideally, these populations would exhibit minimal to no detectable introgression, be relatively robust with a range of age classes, and exist in localities with an array of habitat features between reaches that are conducive to spawning, rearing, and over wintering and summering. Prior to barrier removal or modification, we strongly recommend extensive genetic and habitat evaluations above and below barrier sites. The approach should proceed with caution with the goal of reducing uncertainties through adaptive management. Such an approach will allow managers to weigh relative costs and benefits of barrier removal on a case by case basis. Using a Bayesian network model as a tool to quantitatively weigh the relative risks and benefits of barrier removal may also facilitate the process (Peterson et al. 2008).

While we advocate strategic removal of some barriers, we also believe that maintaining barriers at critical locations within the basin is essential. For instance, Stephens (2007) showed that moderately to highly introgressed individuals continue to persist in the mainstem Little Kern River and select tributaries. Considering the potential use of the mainstem as a migration corridor between tributary junctions, we strongly recommend maintaining or installing barriers at or near tributary-mainstem junctions, while focusing removal or modification efforts to promote passage within tributaries on an experimental basis. This will effectively limit the movement of introgressed or introduced individuals into tributaries, but increase habitat connectivity, encourage gene flow, aid in increasing effective population sizes, and improve genetic heterogeneity within tributaries. Of the fourteen mainstem-tributary junctions within the basin, ten currently have adequate barriers to prevent non-native dispersal (C. McGuire, CDFW, personal communication). From a management perspective, mainstem-tributary confluence barriers strike an important balance between reducing population fragmentation from current levels and increasing habitat connectivity, while also providing an important defense against future introductions.

Establishment of out-of-basin populations

The Little Kern golden trout is an extremely small and isolated population that is restricted to the Little Kern River drainage. Therefore, establishing multiple large allopatric refuge populations outside the drainage could be part of the management strategy. The use of such refuge populations has been successful with other threatened or endangered salmonids such as the Greenback cutthroat trout (*O. clarkii stomias*), Apache trout (*O. apache*), Gila trout (*O. gilae*), and Paiute cutthroat trout (*O. clarkii seleneris*) trout and has several benefits (Harig et al. 2000; Service 2004; Wares et al. 2004). First, out-of-basin refuge populations provide an important insurance against major catastrophic events. For example, a significant wildfire or disease outbreak could cause a major genetic bottleneck, or worse, decimate entire populations within the drainage. Maintaining out-of-basin refuge populations could buffer against such events by preserving genetic integrity and using these individuals to repopulate reaches as necessary. Second, establishing additional source populations would benefit Little Kern golden trout in similar ways to establishing differentiated stocks in segregated headwater reaches. Out-of-basin refuge populations would be isolated from other populations and population differentiation through genetic drift would be encouraged. This would lead to local adaptations among source populations, increase resilience to ecosystem change, and improve species-level genetic diversity and long-term persistence.

We recommend evaluating the establishment out-of-basin Little Kern golden trout populations in remote fishless streams that are in close proximity to the historical range of the species and that exhibit a range of habitat features consistent with those found in the Little Kern River drainage. Introductions should also not threaten persistence of other species, such as invertebrates or amphibians. Critical to establishment of these populations is ensuring both habitat heterogeneity and connectivity exist in order to preserve Little Kern golden trout life history traits and sustain multiple age classes of this species. In their review of greenback cutthroat trout translocations, Harig et al. (2000) found most translocation failures that were not associated with invasions of non-native fishes were the result of a lack of habitat quality or quantity; they also found that long continuous reaches of habitat were most likely to support robust, self-sustaining populations. Harig and Fausch (2002) found that water temperature, wetted width, and pool habitat were strong limiting factors in establishing translocated populations of Greenback and Rio Grande cutthroat trout populations and other authors have come to similar conclusions (Hilderbrand and Kershner 2000). Establishing refuge populations in close proximity to the Little Kern River with suitable habitat heterogeneity ensures that environmental selection pressure and evolved life history traits remain compatible and genetic diversity is preserved (and potentially augmented). Most importantly, however, threats to the long term persistence of Little Kern golden trout from demographic or environmental stochasticity are reduced.

Discussion

New threats to populations often develop in response to management actions designed to alleviate some long-standing cause of decline. This is well illustrated by the Little Kern golden trout, where management actions ameliorated an initial threat of hybridization, but led to unexpected threats associated with genetic structuring and low genetic diversity. The new threats evolved over a course of 30 years, a pattern seen in other endemic trout populations.

The changing nature of threats as mediated by management appears more common than previously recognized. In our review of other trout conservation efforts (Table 3), we found several subspecies of inland cutthroat trout that were fragmented by barriers due to the threat of introgression or competitive displacement from introduced fishes. Introgressive hybridization has played a prominent role in the demise of most inland cutthroat trout populations and barriers, chemical eradication, and hatchery supplementation are common strategies used to ameliorate this threat (Behnke 1992, 2002). As with Little Kern golden trout, these strategies arguably reduced risk of extirpation associated with the initial threat posed by introduced fishes, but evolved threats were triggered by management actions. In some of these subspecies accounts, it was not entirely clear if population fragmentation was the result of isolation, range reductions from competitive displacement and hybridization, or a combination of the two. For instance, the Rio Grande cutthroat trout (*O. clarkii virginalis*) experienced range reductions of nearly 95 % (Behnke 2002), and similar to Little Kern golden trout, it also was restricted to small headwater streams isolated by barriers. However, conservation management strategies have also purposely isolated Rio Grande cutthroat trout populations in order to reduce hybridization rates with non-native trout and this has resulted in declines in genetic heterogeneity (Pritchard et al. 2007).

While this paper focuses on trout, conservation histories from other species may also fall under the umbrella of threat evolution. For instance, conservation interventions (e.g., vaccinations and tagging) to alleviate an initial threat of disease in African wild dog (*Lycaon pictus*) populations have led to stress disorders and possible extinctions (Burrows et al. 1994). The use of hatchery-reared salmon to augment depressed wild populations has been shown to improve relative abundance, but a multitude of new threats have emerged including a proliferation of disease, a decline in fitness, loss of genetic heterogeneity, and shifts in behavioral adaptations (Chilcote et al. 2011; Naish et al. 2013; Snyder et al. 1996). Captive breeding of the black robin (*Petroica traveri)* successfully enhanced depleted population densities, but management intervention increased the frequency of a maladaptive trait (Massaro et al. 2013). The concept of threat evolution has not received ample attention, yet we believe it reaches across taxonomic boundaries.

Understanding how threats evolve and how species or populations respond in the long term to particular management actions is a critical, yet often overlooked component of conservation biology and species recovery. The well-documented management history of Little Kern golden trout and more specifically, the evolution of threats mediated by management action highlight an important potential pitfall for other imperiled species. Fully understanding the temporal consequences of management strategy on a species-by-species basis may be extremely time consuming and costly. However, defining the temporal extent to which a particular strategy is effective and adapting that strategy through time as threats evolve is critical to our understanding of species' response to management and our ability to advance species recovery. Due to the broad overlap in ecology, life history, and management of Little Kern golden trout and many other inland salmonids, we believe that the evolution of threats discussed here is relevant to similarly managed species and can help resource managers assess the potential costs and benefits associated with such strategies within a regional context.

Management strategies rarely exist in perpetuity and often must be made in the face of considerable uncertainty about the species ecology. Here, we argue that initial management actions intended to ameliorate known threats can lead to emergence of new threats as a direct consequence of the interventions employed; however, we are not suggesting inaction in the face of uncertainty and potential emergent threats. We believe that immediate management intervention is often necessary to prevent significant declines in threatened populations and suggest that adaptive management within a structure decision making framework can improve understanding of the relationships between initial management actions and evolution of downstream threats and ultimately lead to improved conservation outcomes. Through decision analysis tools, such as structured decision making, managers can identify areas of uncertainty and evaluate the risks and benefits of each management alternative in a transparent way (Gregory et al. 2012a, b). In this context, adaptive management can allow for iterative decision making as new ecological information is gathered through monitoring and targeted research and can help identify evolved threats and inflection points in management where continued actions to address initial threats should be halted in favor of actions that address evolved threats.

Table 3 Examples from inland trout management that show feedbacks between an initial threat and management action that produces a new threat

Species	Species status	Initial threat	Management action	Evolved threat	References
Little Kern golden trout (*Oncorhynchus mykiss whitei*)	Threatened	Hybridization and competition with non-natives	Fish passage barriers, chemical removal, restocking	Genetic structure, low heterozygosity	Stephens (2007)
Colorado cutthroat trout (*Oncorhynchus clarkii pleuriticus*)	Species of concern	Hybridization and competition with non-natives	Fish passage barriers	Low habitat heterogeneity/connectivity	Novinger and Rahel (2003)
Colorado cutthroat trout (*Oncorhynchus clarkii pleuriticus*)	Species of concern	Hybridization and competition with non-natives	Fish passage barriers	Lack of habitat size to sustain effective population sizes	Hildebrand and Kershner (2000)
Greenback cutthroat trout (*Oncorhynchus clarki stomias*)	Threatened	Hybridization and competition with non-natives	Translocations	Lack of habitat suitability and size	Harig et al. (2000)
Bonneville cutthroat trout (*Oncorhynchus clarki utah*)	Species of concern	Hybridization and competition with non-natives	Fish passage barriers	Lack of habitat size to sustain effective population sizes	Hildebrand and Kershner (2000)
Westslope cutthroat trout (*Oncorhynchus clarkii lewisi*)	Species of concern	Hybridization and competition with non-natives	Fish passage barriers	Lack of habitat size to sustain effective population sizes	Hildebrand and Kershner (2000)
Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*)	Species of concern	Hybridization and competition with non-natives	Fish passage barriers	Small effective population size, genetic threats.	Kruse et al. (2000)
Pauite cutthroat trout (*Oncorhynchus clarkii seleniris*)	Threatened	Hybridization	Chemical removal and restocking	Low genetic diversity	Cordes et al. (2004)
Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*)	Species of concern	Hybridization and competition with non-natives	Fish passage barriers	Low genetic diversity	Behnke (1992), Pritchard et al. (2007)

The Little Kern golden trout and other imperiled species will benefit from long-term, tiered conservation planning within an adaptive management framework that recognizes evolving threats and changing conditions in order to increase the likelihood of species persistence and recovery. Each species will require its own site-specific management objectives and actions, but set within the context of a broader long-term dynamic ecological framework. A long-term strategic vision of the evolving dynamics between management and species response should strongly be pursued.

Acknowledgments The manuscript benefitted from the review of two anonymous reviewers and countless colleagues. We would like to thank Bjorn Erickson and Karrigan Bork for insight regarding management trends in other species and the US Fish and Wildlife Service Pathways Program. Finally, we would like to thank all the fish biologists that have worked and continue to work on the Little Kern golden trout.

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