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RESEARCH PAPER

Long-term captive breeding does not necessarily prevent reestablishment: lessons learned from Eagle Lake rainbow trout

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Abstract Captive breeding of animals is often cited as an important tool in conservation, especially for fishes, but there are few reports of long-term (<50 years) success of captive breeding programs, even in salmonid fishes. Here we describe the captive breeding program for Eagle Lake rainbow trout, *Oncorhynchus mykiss aquilarum*, which is endemic to the Eagle Lake watershed of northeastern California. The population in Eagle Lake has been dependent on captive breeding for more than 60 years and supports a trophy fishery in the lake. Nevertheless, the basic life history, ecological, and genetic traits of the subspecies still seem to be mostly intact. Although management has apparently minimized negative effects of hatchery rearing, reestablishing a wild population would ensure maintenance of its distinctive life history and its value for future use as a hatchery fish. An important factor that makes reestablishment possible is that the habitat in Eagle Lake is still intact and that Pine Creek, its major spawning stream, is recovering as habitat. With the exception of an abundant alien brook trout (*Salvelinus fontinalis*) population in Pine Creek, the habitat factors that led to the presumed near-extinction of Eagle Lake rainbow trout in the early twentieth century have been ameliorated, although the final stages of reestablishment (eradication of brook trout, unequivocal demonstration of successful spawning migration) have still not been completed. The Eagle Lake rainbow trout story shows that long-term captive breeding of migratory salmonid fishes does not necessarily prevent reestablishment of wild populations, provided effort is made to counter the effects of hatchery selection and that natural habitats are restored for reintroduction. Long-term success, however, ultimately depends upon eliminating hatchery influences on wild-spawning populations. Extinction of Eagle Lake rainbow trout as a wild species becomes increasingly likely if we fail to act boldly to protect it and the Eagle Lake watershed.

Keywords Salmonidae · Captive breeding · Hatchery effects · Species invasions · Endangered species · Conservation · Eagle Lake

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Introduction

Captive breeding of animals is often cited as an important tool in conservation (Soulé et al. 1986), especially for fish (Phillippart 1995). In some cases, it

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is the final resort for the species, when the last individuals are taken into captivity, as has happened with California condor (*Gymnogyps californianus*), black-footed ferret (*Mustela nigripes*), Arabian oryx (*Oryx leucoryx*), European bison (*Bison bonasus*), and Owens pupfish (*Cyprinodon radiosus*) (Miller and Pister 1971; Kleiman 1989; Snyder and Snyder 2000; Perzanowski and Olech 2007; Belant et al. 2011). Most captive breeding programs, however, are fairly recent in origin and have little long-term experience with reestablishing wild populations. A general goal of captive breeding is to re-establish species in the wild once suitable habitat is available, although this is not always possible (Snyder et al. 1996). Major concerns include loss of fitness for survival in the wild during captivity, through loss of genetic diversity, selection for traits that improve survival in captivity but are detrimental in the wild, and loss of learned behaviors essential for survival in the wild (Busack and Currens 1995; Araki et al. 2007, 2008).

Many hatchery programs for fishes of the family Salmonidae (salmon, trout, charrs, etc.) are arguably captive breeding on a large scale, although they are mostly designed to supplement existing wild populations or to support fisheries directly (Hilborn 1992; Busack and Currens 1995). Fish used for the latter purpose can become completely domesticated (Moyle 1969; Huntingford 2004); they are raised to be caught shortly after release (put-and-take fishery) or are released into fairly benign conditions, such as ponds or reservoirs, with no expectation of natural reproduction (put-and-grow fishery). Fish from supplementation hatcheries, however, are expected to survive in the wild although mortality rates once released are usually extremely high. Nevertheless, supplementation programs have shown considerable success in maintaining fisheries but their long-term prospects have been questioned (Fraser 2008; Kostow 2008). One reason for concern is loss of fitness for survival in the wild, which in steelhead (*Oncorhynchus mykiss*) can be significant in 1–2 generations (Araki et al. 2007, 2008, 2009). Fraser (2008) points out that there is little evidence that salmonids with a long hatchery history can establish self-sustaining wild populations. Most of the evidence is equivocal or anecdotal. However, Chilcote et al. (2011) show that wild populations of three species of anadromous salmonids have greatly reduced ability to be self-sustaining when fish of hatchery origin are also present.

An unusual opportunity to see if a salmonid population long maintained by captive breeding can revert to a wild, self-sustaining state is found in Eagle Lake rainbow trout (*Oncorhynchus mykiss aquilarum*). This trout is endemic to a single California watershed but is now in widespread use in the western USA as a hatchery fish. It has been reared in captivity for the first year or more of life for more than 60 years and is stocked annually into its native Eagle Lake, California, to support a trophy fishery (Moyle 2002). The stocked fish, once mature, are captured, spawned, and returned to Eagle Lake. Some of their progeny are used as brood stock for part of the hatchery program. In this respect the captive breeding program for Eagle Lake rainbow trout (ELRT) has characteristics of both a supplementation hatchery program and a put-and-grow program. While the hatchery program probably saved ELRT from extinction, its principal purpose has been to maintain the sport fishery in Eagle Lake and in other water bodies in California. Access of ELRT to their major former spawning tributary (Pine Creek) has been completely blocked to allow for easy capture of mature fish. Moyle et al. (2008) suggested that the ELRT should be listed as a threatened species because of its complete dependence on hatchery rearing for survival.

In this paper, we (1) describe the distinctive nature of Eagle Lake and its watershed, (2) review the biology, history, and recent studies of ELRT, and (3) present new information on ELRT life history and genetics. We then use this information to answer the following questions:

- Can a self-sustaining population of ELRT be re-established in its native habitats after nearly 60 years of captive breeding?
- If so, what changes in management of ELRT are required in order to re-establish a self-sustaining population in the Eagle Lake watershed?

Finally, we discuss insights gained from this study in the use of captive breeding for restoration of native fish.

Eagle Lake and its watershed

Eagle Lake (40.6 N, 120.7 W) is the second largest natural lake (24 km long by 3–4 km wide) entirely contained in California, with a surface area of ca. 8,900 ha (Fig. 1). It is situated in northeastern

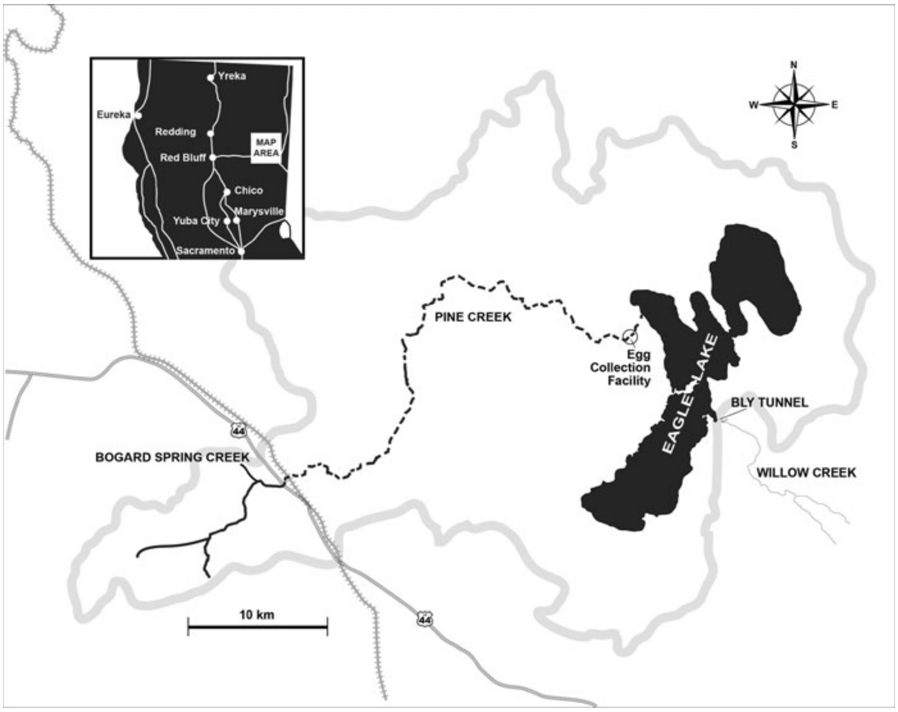

Fig. 1 Eagle Lake basin, showing the location of Pine Creek, the principal spawning tributary of Eagle Lake rainbow trout, and of Bogard Spring Creek, a small tributary at the lower end of the permanent reaches of Pine Creek, that is used for experimental spawning and rearing. Stream sections shown by a *dashed line* are usually dry in summer. The uppermost ca. 5 km of Pine Creek, which are highly seasonal in flow, are not shown

California at an elevation of about 1,555 m (lake surface elevation varies with inflow). This endorheic (terminal) lake consists of three basins, two of them averaging 5–6 m deep, the third averaging 10–20 m with a maximum depth of about 23 m. The shallow basins are similar in their limnology and water temperatures sometimes exceed 21°C in the summer, although the deep basin stratifies, providing a cool water refuge for trout. The lake is highly alkaline (pH 8.4–9.6) with alkalinity increasing during dry periods as lake levels decline (Huntsinger and Maslin 1976).

The fish species present in Eagle Lake are all native: ELRT, tui chub (*Siphateles bicolor*), Lahontan redside (*Richardsonius egregius*), speckled dace (*Rhinichthys osculus*) and Tahoe sucker (*Catostomus tahoensis*). Eagle Lake is the only large lake in California without alien species (Moyle 2002), although more than 11 alien fishes were stocked at various times (Table 1). Most of the species failed to become established and those that did disappeared from the lake during periods when lake levels were low and pH levels were high, presumably inhibiting reproduction (Purdy 1988).

Table 1 Species, year and fish stocked in Eagle Lake since 1924 (King and Weidlein, unpublished data, 1976; Purdy 1988; Pustejovsky 2007)

Species	Year	No of fish stocked
Coregonus clupeaformis	1879	225,000
Ameierus nebulosus	1879	–
Micropterus salmoides	1901–1902/1930	1047
Salmo trutta	1914/1931–1933	310,000
Oncorhynchus mykiss	1920's/1932/1953	>21,000
Salvelinus namaycush	1924	25,000
Pomoxis spp.	1930	150
Lepomis macrochirus	1930	650
Oncorhynchus kisutch	1934–1935	478,416
Oncorhynchus nerka	1952–1956	886,750
Salmo clarkii henshawi	1955–1956	243,200
Oncorhynchus mykiss aquilarium	1953/1956/ 1960–now	10–15 million

All introductions ultimately failed

Pine Creek is the main tributary of Eagle Lake with a length of approximately 63 km, of which only ca. 11 km are considered perennial today, although it is possible that the perennial reach was longer in the past. The Pine Creek watershed covers 591 square km and makes up 65% of the total surface inflow into Eagle Lake. The creek starts at the outflow of Triangle Lake at about 2,200 m elevation, although the perennial reach does not start until about 5 km downstream, with a major spring system. Snowfall is the dominant form of precipitation and varies from 46 to 152 cm per year (Young 1989). More than 21 headwater springs (DFG 1998) contribute to the Pine Creek summer flows, including water from Bogard Spring Creek, the lowermost spring tributary. Bogard Spring Creek, presumably was once an important spawning tributary for ELRT; even during recent (2007–2010) relatively dry years, it had average summer flows of 0.015 m^3/s, through low gradient meadows and slightly steeper forested reaches (Carmona-Catot et al. 2010). The perennial reach of Pine Creek is a cold (summer temperatures <20°C) spring-fed stream, with summer flows of 0.03–0.14 m^3/s through meadows and open forest, with modest gradients and moderately deep (<1 m) pools. The banks are covered by sedges and grasses with areas of willows (*Salix* spp.) and other riparian shrubs, and the adjacent forest lands are dominated with mixed conifers (*Pinus* spp.) and quaking aspen (*Populus tremuloides*) (Pustejovsky 2007).

Pine Creek typically connects to the lake during March–May, with flows produced by the spring snow melt. The lower 35–40 km of stream channel mostly meanders through open 'flats' dominated by sagebrush and other shrubs, with only occasional pools that last into the summer. This historic condition of this lower reach is uncertain (Young 1989) although the watershed was subject to heavy grazing and logging, as well as impoundment and diversion of water for much of its recent history, causing degradation of many areas (Pustejovsky 2007).

Dominant fish in Pine Creek are alien brook trout (*Salvelinus fontinalis*) which occur at extremely high densities. In addition, small numbers of native Tahoe sucker, Lahontan redside and speckled dace are present (Carmona-Catot et al. 2010). The occurrence of ELRT is described in the next section. There are no records of brook trout from Eagle Lake itself (Moyle 2002).

Eagle Lake rainbow trout

Biology

ELRT are endemic to Eagle Lake, and historically depended on Pine Creek for spawning. They are the only rainbow trout native to the Great Basin, the vast area between the Rocky Mountains and the Sierra Nevada (Behnke 2002). Snyder (1917) described this trout as a subspecies of rainbow trout (*Salmo gairdneri aquilarum*). In an extensive electrophoretic, karyotypic, and meristic analysis, Busack et al. (1980) validated Snyder's determination. Recent genetic studies (DNA sequence data) further demonstrate the distinctiveness of ELRT and indicate that its closest relatives are rainbow trout in the Feather River, which has headwaters west of Eagle Lake (Simmons 2011). Behnke (2002) speculated that the Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) was the original trout of Eagle Lake, but it became extinct in the Pleistocene during a long drought. Presumably rainbow trout invaded through an unspecified headwater connection during a wetter period.

ELRT show many adaptations for living in a highly alkaline desert lake. They are found generally throughout the lake, and have been observed foraging in shallow water at temperatures of 22–23°C, although they usually seek cooler deep waters when surface temperatures are high. The pH tolerances (up to 9.6) of ELRT are high for a trout but similar to other Great Basin trout (Moyle 2002). They forage on Eagle Lake's abundant zooplankton and benthos early in summer, but switch largely to feeding on fish, especially young-of-year tui chubs, as they become abundant in late summer (Moyle 2002; Eagles-Smith 2006). Based on growth of yearling fish from hatchery plantings in the lake, wild fish presumably grew to about 40 cm FL by the end of their first year in the lake, 45–55 cm FL in the third, and up to 60 cm FL in the fifth year. ELRT historically grew to 3–4 kg and 65–70 cm FL (McAfee 1966). Rapid growth was the result of abundant forage combined with a delay in maturity until 2–3 years of age. This latter trait has made them highly desirable as a hatchery fish (Dean and Chapell 2005).

As far as we can piece together from historic records, present life history traits, and recent studies, ELRT life history was much like that of anadromous rainbow trout (steelhead). We speculate the basic life history was as follows: after growing to a large size (50+ cm FL) in the lake, at ages 2 or 3, ELRT would mature and congregate at the mouth of Pine Creek in March. If stream flows were adequate, the fish would migrate 45–55 km upstream to spawn, and then return to the lake, if not stranded by rapid drops in flow. Juveniles would rear in the creek for 1–2 years before moving out to the lake. If stream flows were low, adults would not migrate and wait another year. The unusually long life span of ELRT (up to 11 years, McAfee 1966; G. Carmona-Catot, unpublished data) suggests that they could delay reproduction repeatedly to survive periods of drought. It is also likely, however, that a resident population of smaller individuals was present in Pine Creek, providing some juveniles to out-migrate to the lake. While speculative, this flexible life history is found in anadromous rainbow trout (steelhead, *O. mykiss*) in California (Moyle et al. 2008) and some other lake-dwelling rainbow trout populations, such as Goose Lake redband trout (*O. m. newberrii*, Moyle 2002). Another life history option is suggested by observations that spawning can take place in the intermittent sections of stream followed by immediate movement of fry to the lake. In 2010, 26 adult spawners were released into the lower creek in April, as flows were dropping. Subsequently, fry (30–40 mm TL) were collected from the trap downstream in June (P. Divine, California Department of Fish and Game (DFG), pers. comm.). Whether these fish can survive in the lake is not known.

History

The first records of ELRT demonstrate their former abundance. According to Purdy (1988), "In the spring months of the 1870s and 1880s, when trout were spawning, huge quantities were being caught. It was not unusual to hear that wagon loads of trout, some weighing as much as 600 lb, were being brought into Susanville where they were sold at local markets for twenty-five cents a pound (p. 14)." This high abundance of fish attracted many predatory birds, including osprey, bald eagles, white pelicans and other species (Sheldon 1907). When the ELRT was described by Snyder (1917), he noted its numbers were already low. While commercial fishing for the trout was banned in 1917, poaching of vulnerable spawners no doubt continued. This exploitation, which contributed to the decline of ELRT, occurred at the same time as extensive logging in the drainage, heavy grazing in the meadows, and construction of railroads and roads across the meadows and streams.

Timber harvesting officially started in Lassen National Forest in 1909 although the highest production took place in the 1970s and 1980s (US Department of Agriculture 2005). The direct effects of timber harvest may have been small because of the rapid infiltration capacity of the volcanic soils of the region, reducing erosion (Platts and Jensen 1991). However, logging did create erosion-prone roads, and resulted in railroads being constructed across the Pine Creek drainage in the 1930s and 1940s, restricting flow of the creek and channelizing the streambed. This situation was exacerbated when highway 44 was built alongside the railroad and the creek was restricted by culverts. The combination of culverts and channelized stream created a barrier to spawning adults in the spring.

Livestock grazing started in the mid 1800s and was unregulated until 1905. Grazing livestock have been a major problem because cattle tend to gather around and in the creeks, although the problem is diminished today because of better management of grazing (Pustejovsky 2007). However, the legacy effects of intensive grazing continue. For the lower 40 km of Pine Creek, the stream bed was frequently down cut and enlarged, much of the riparian vegetation was removed, and riparian meadows increasingly became dry flats dominated by sagebrush. Presumably as a result, flows in lower Pine Creek became increasingly intermittent during summer, with spring flows decreasing more rapidly after the snowmelt. As a consequence, spawning adult ELRT would have had reduced access to the key spawning and rearing areas and would have been more exposed to predators and poachers during migration. Between 1940 and 1949, brook trout were introduced into Pine Creek and became extremely abundant.

In the 1920s, Bly Tunnel was constructed to deliver water from Eagle Lake to Willow Creek for use by farms downstream (Moyle et al. 1991; Purdy 1988). While the water delivery scheme failed, during the 1930s lake levels dropped as the result of diversion of water through the tunnel in combination with a severe prolonged drought, which presumably reduced access of spawning trout to Pine Creek.

As a result of all these factors, ELRT became drastically diminished in the early twentieth century. In 1931, Snyder observed low numbers of trout in the lake and Pine Creek (Snyder 1940) and in 1939 biologists in Lassen National Forest expressed concern over impoundments further reducing flows of the creek (Pustejovsky 2007). In 1949 and 1950, DFG collected 35 and 75 adult ELRT, respectively, from the mouth of Pine Creek, spawning them for hatchery rearing (Dean and Chapell 2005). The 258 progeny from the 1949 fish were planted in Pine Creek, where brook trout had recently become established, so probably did not survive. The spawning of fish in 1950 was more successful and the hatchery-reared progeny were planted in the embayment at the mouth of Pine Creek. In 1951–1958, some artificial propagation also took place although the records are not clear as to how much (Dean and Chapell 2005). Prior to hatchery propagation, trout presumably persisted only because occasional wet years permitted successful spawning despite degraded stream channels and the presence of brook trout in the spawning reaches (McAfee 1966). It is possible that these actions by DFG biologists prevented extinction of ELRT although it is equally possible, based on recent genetic evidence, that a small population persisted until all access to upstream areas was blocked.

In 1959, an egg taking station was built at the mouth of Pine Creek, including a wooden weir/dam to block upstream passage of most fish (Dean and Chapell 2005). Regular trapping operations began in 1959, when 16 trout were captured and spawned; in the next 5 years the numbers captured varied from 45 to 391 (McAfee 1966). From 1959 through 1994, a few trout were able to make it over the barrier during wet years, allowing some successful natural spawning (Pustejovsky 2007; Moyle, unpublished data).

In 1995, the weir was rebuilt to prevent migration of ELRT to upstream areas (Pustejovsky 2007). The early life history of the trout then became almost entirely under human control. At present, eggs and milt are stripped from fish at the egg taking station; the embryos are then transported to Crystal Lake Hatchery, from where they are distributed to other hatcheries across California (Fig. 2). Originally, trout were marked to prevent using fish from being used more than once for spawning, to prevent sibling crosses in order to minimize inbreeding, and to select

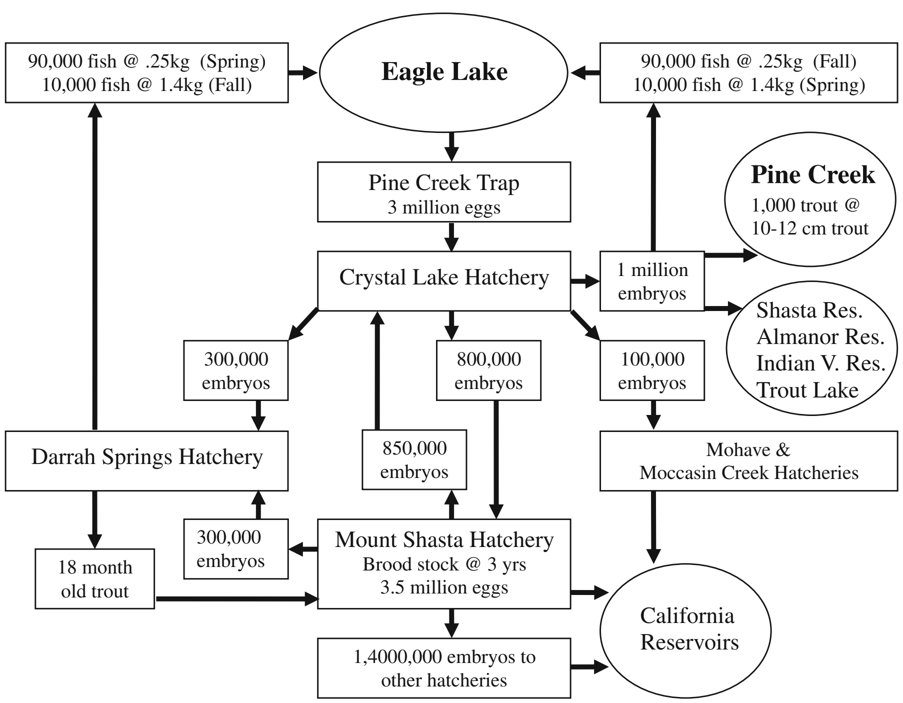

Fig. 2 Distribution of ELRT through California's hatchery system in 2006, as a representative year. The numbers shift from year to year based on the number of eggs that are collected at Pine Creek and the needs within the State (DFG, unpublished data; Dean and Chapell 2005). Once fertilized eggs of ELRT are distributed to hatcheries, the fish are reared for a year or more in the hatcheries. Most are planted at lengths at which they can grow rapidly to harvestable size in Eagle Lake or in reservoirs or at lengths at which they can be available for immediate harvest. Some individuals are retained in hatcheries for use as brood stock for generation of more domesticated progeny

for longer lived fish to compensate for longevity reductions that may have been caused by past hatchery practices (R. L. Elliott, DFG, pers. comm., 1998). Today, the main process is simply to stock only progeny of wild-trapped fish in the lake. At the Mount Shasta Hatchery, broodstock trout are reared from eggs collected at the Pine Creek egg taking station; once mature, the broodstock are used for multiple spawning seasons to produce trout which are stocked widely across California, mainly in reservoirs. Although progeny of first generation broodstock were planted in Eagle Lake in the past, DFG currently stocks only trout from the eggs annually collected at the station (P. Divine, DFG, pers. comm. 2009; DFG, unpublished data). Each year, approximately 180,000–200,000 trout weighing about 0.23 kg (0.5 lb) each and 20,000 1 kg + "trophy fish" are stocked in Eagle Lake for the fishery. Prior to 2006, in some years, DFG also has stocked ca. 1,000 "half pound" fish in Pine Creek to reduce the brook trout population through predation (Dean and Chapell 2005), although there were no studies to confirm that it worked. Subsequent sampling suggests that few of these fish persisted long in the creek (Moyle, unpublished data).

Recent studies

In 1987 a Coordinated Resource Management Planning (CRMP) group of stakeholders was organized to develop and implement a plan for restoring Pine Creek. The Pine Creek CRMP process resulted in reducing sedimentation from of roads, improving riparian areas, eliminating a diversion, fencing long reaches of creek, obtaining a conservation easement on key private land, replacing culverts with more fish-friendly passage structures, and constructing a fish ladder to provide access to upper spring habitat (Pustejovsky 2007). The major problems remaining are getting adult ELRT access to the habitat and to eliminate or reduce the problem of non-native brook trout.

Life history

Despite the long history of hatchery selection, there is evidence that ELRT can still spawn successfully in Pine Creek. Adults that were trucked to the upper reaches of the creek in 2005–2008 (DFG unpublished), produced young which survived and grew for 2–4 years. In 2007–2009, we conducted thorough surveys (electrofishing and snorkeling) within the perennial portion of the Pine Creek to determine distribution and abundance of wild ELRT. Only 22 ELRT were seen in the more than 4.5 km sampled and 3 years of study, amidst hundreds of brook trout. Although ELRT numbers were small, they suggest some successful spawning and rearing is possible despite abundant brook trout.

In a 3-year brook trout removal project conducted along the entire 2.8 km of Bogard Spring Creek, 7,264 fish were captured (Carmona-Catot et al. 2010). Of these, 3% were ELRT, 92% brook trout, 4% speckled dace, and 1% Tahoe sucker. ELRT juveniles were present mainly at the middle and lower sites; 169 were captured in 2007, 25 in 2008, and 34 in 2009. From April to August, three 50 m sites were snorkeled every month, counting a total of 26 ELRT, 488 brook trout, and eight minnows. In spring 2009, a UC Davis-DFG-US Forest Service (USFS) crew captured 30 mature ELRT from the mouth of Pine Creek and transported them to Bogard Spring Creek, now depleted of most of its brook trout. Redds were observed soon after and in visual surveys in June and July, 250 ELRT fry were observed (Moyle and Carmona-Catot, unpublished observations).

In 2007 and 2008, we examined the scales of 71 of 194 wild ELRT captured in Bogard Spring Creek to determine age from annuli. Ages were validated based on lengths and the likelihood that strong seasonal patterns of temperature and flow would produce annual marks (DeVries and Frie 1996). We found that age 1+ fish grew until approximately 80 mm FL, age 2+ fish until 160 mm FL, and age 3+ until 180 mm FL; the only age 4 fish captured measured 218 mm FL (Fig. 3). These numbers are consistent with a stream population of rainbow trout (Moyle 2002) and indicate either rapid establishment of a resident population or delayed emigration of larger fish or both.

The spawning migration of ELRT began to be studied in 1999 by the Pine Creek CRMP. Radio-tracking studies were conducted every year until 2005 (except 2003) and, in 2007 and 2008, they switched to tracking with passive integrated transponder (PIT) tags. The aims of these studies were to evaluate the effectiveness of stream channel restoration projects and determine if ELRT could reach the spawning

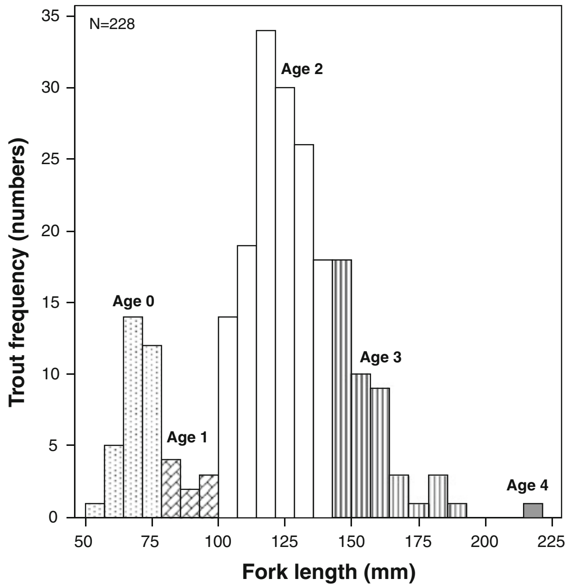

Fig. 3 Fork lengths and ages of Eagle Lake rainbow trout in Bogard Spring Creek sampled in 2007, 2008, and 2009. Age distributions are inferred from scales of 71 fish

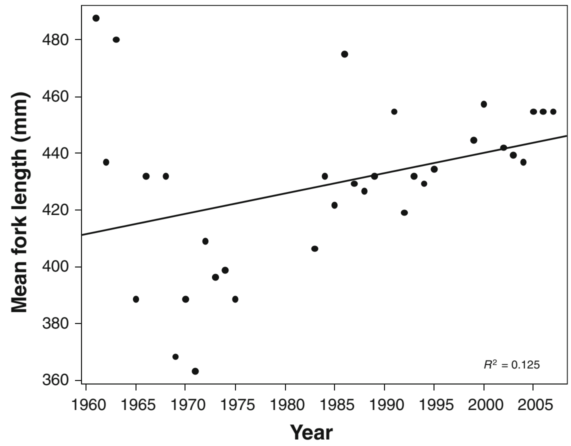

Fig. 4 Mean fork length of the Eagle Lake rainbow trout taken in the sport fishery at Eagle Lake (King 1976; DFG 2005, unpublished data; Pustejovsky 2007)

grounds of Pine Creek. ELRT were collected during the spawning season at the Pine Creek fish trap, transmitters were inserted and crews searched for signals of tagged fish to monitor their upstream migration. For a variety of reasons, including demand for eggs by hatcheries, numbers of tagged fish were small (n = 10–51) and releases occurred late in the season when stream flows were low and fish were ripe (running eggs and milt). No fish was ever detected beyond km 27 of the 40 km trip necessary to reach the suitable habitat for spawning. However, in June 1999, a single radio transmitter was recovered in the upper reaches of the main tributary of Pine Creek, and in 2011, a singe adult male managed to make his way from the trap to the upper creek (T. Pustejovsky, pers. comm.). Unfortunately, hatchery priorities have often precluded the availability of sufficient ELRT spawners for conducting more robust studies on the upstream migration and possibilities of restoring a natural run (Thompson et al. 2007; G. Carmona-Catot, pers. obs., 2007, 2008).

Population data for ELRT in the lake is very scarce, and it is dependent on the stocking allotments every year. Creel census data indicated that catch per hour from 1983 through 2007 ranged from 0.2 to 0.6, with a mean of 0.3, while average fork length (FL) of fish caught increased over the years (Fig. 4). The number of mature females captured at the trap while migrating and spawned by the DFG ranged from ca 600 to 1,700, although estimates were made of size of the entire spawning run. The number of eggs collected averages about 2.2 million, with annual takes of 607,000 to 6 million eggs (P. Divine, DFG. pers. comm.); the egg quotas are developed every year by DFG hatchery personnel in order to achieve the hatchery goals. The mean egg size and the number of eggs per female have showed little change, 2000–2010, although DFG selects for larger fish (Table 2).

Genetics

The population genetics of ELRT was investigated using eleven microsatellite loci. The methods are described in detail in Simmons (2011) and are briefly summarized here. Fin clips were taken from individuals from the Eagle Lake fishery. Genomic DNA was extracted from 84 fin clips using the Puregene extraction kit (Promega). After touchdown PCR, 1 μL PCR product was combined with 0.2 μL LIZ600 ladder (Applied Biosystems) and 8.8 μL highly deionized formamide then visualized on an ABI 3130xl capillary system. Alleles were scored using Genemapper version 4.0 (Applied Biosystems).

Fstat v. 2.9.3.2 (Goudet 1995) was used to calculate Weir and Cockerham's (1984) F-statistics. LDNE (Waples and Do 2008) was used to calculated effective population size by measuring linkage

Table 2 Number of eggs collected, mean egg size, eggs per female and total number of females spawned each year at the DFG egg station in Pine Creek (Crystal Lake Hatchery, unpublished data, 2010). For spawner sorting at the trap, DFG distinguishes between "select" fish (S) which are females greater than 508 mm in fork length and the rest of the females (T). The size classes were not distinguished in 2008–2010

Year	Female classification	No eggs collected × 1,000	Mean egg size (mm)	No eggs per female	No females spawned
2000	S	1,713	6.10	3,976	431
	T	1,393	7.04	3,563	391
	Total	3,106	6.58	3,769	822
2001	S	1,458	5.99	3,664	398
	T	1,524	6.50	3,019	505
	Total	2,982	6.25	3,341	903
2002	S	2,632	6.60	3,625	726
2003	S	1,063	6.55	3,739	284
	T	2,007	6.78	3,023	664
	Total	3,070	6.65	3,381	948
2004	S	1,274	6.65	3,932	335
	T	1,946	7.06	2,944	650
	Total	3,220	6.86	3,438	985
2005	S	651	6.58	3,125	212
	T	1,315	7.34	2,914	457
	Total	1,966	6.96	3,020	669
2006	S	1,055	6.73	3,087	390
	T	2,157	6.91	2,754	776
	Total	3,212	6.83	2,921	1,166
2007	S	1,114	6.60	2,971	386
	T	2,354	7.01	2,688	874
	Total	3,468	6.81	2,830	1,260
2008	–	2,757	7.16	3,156	858
2009	–	5,986	7.09	3,429	1,737
2010	–	1,940	–	2,904	668

disequilibrium, and to perform a jackknife across loci for 95% confidence intervals. Alleles with a frequency below 0.05 were excluded from the analysis, as extremely low frequency alleles have been shown to bias N_e estimates (Waples 2006 and references therein). The program Bottleneck (Cornuet and Luikart 1997) was used to assess the probability that a given population had undergone a recent demographic bottleneck under the two-phase model with default parameters.

We found individuals in the lake population had an F_{IS} or inbreeding value, of 0.064, significantly higher than zero, although no genetic evidence of a bottleneck was detected. The effective population size was estimated at 1,125 fish, with a confidence interval from 151–∞, indicating that in all years there was a large population contributing to reproduction. Even a conservative estimate of effective population size is higher than the number of individuals presumed to have founded the hatchery population. Given that small estimate of founders, it is interesting that no genetic bottleneck was detected. The original bottleneck could have been masked by the number of generations that have passed since the bottleneck and efforts in the hatchery breeding program to maximize genetic diversity, as seen in the population's now high effective population size. It is also possible that the population left in the lake in the 1950s was larger than sampling efforts on Pine Creek indicated and multiple years of naturally-spawned fish contributed to the initial hatchery stock. The slight if significant F_{IS} value is still something to be concerned about and to monitor, although it is comparable to levels found in other lake-stream systems in the region such as Goose Lake (Simmons 2011). The steady increase in average size of trout caught may reflect selection for fast growth and large size, as indicated by the tendency of hatchery personnel to favor larger females for breeding (Table 2). However, changes in fish regulations may also contribute to increased size in the catch (P. Divine, DFG, pers. comm.).

Discussion

- **Can a self-sustaining population of ELRT be re-established in its native habitats after nearly 60 years of captive breeding?**

There are four reasons why the answer to this question is most likely a strong "yes:" (1) The basic ecological relationships of ELRT in Eagle Lake itself are still intact. (2) ELRT seem to have retained their migratory life history pattern. (3) ELRT are still reasonably diverse genetically. (4) Their historic habitat is still basically in good condition and is improving with restoration efforts.

Lake ecology

ELRT in Eagle Lake still behave in a surprisingly natural fashion, feeding readily on abundant natural prey, foraging and living in appropriate parts of the lake according to temperature and other factors, and aggregating at the mouth of Pine Creek (and other smaller creeks) in the spring for spawning. Growth is fairly rapid and consistent over the years. Part of the reason for this is the abundance of invertebrates and small fish as food for the predatory trout (Moyle 2002; Eagles-Smith 2006) although for this same reason the lake also supports an abundance of avian predators such as osprey and white pelicans (Lederer 1976). The major source of mortality for ELRT, once they have survived the initial planting, however, is presumably angler harvest.

Life history

The most likely pattern for ELRT life history under historic conditions was centered around a large population of large fish in Eagle Lake that migrated up Pine Creek to spawn in spring during years of sufficient flow from snow melt. The young likely reared in the highly productive tributary streams for 1–3 years before returning to the lake. ELRT had two adaptations to make sure this strategy could result in their persistence over long periods of drought: exceptional longevity (for a trout) and presumed presence of a resident population in the headwater springs, that could re-colonize the lake under a complete disaster scenario or maintain genetic diversity through times of low lake populations. This complex life history pattern is basically the same as that adopted by many populations of steelhead rainbow trout in coastal California (Moyle 2002).

ELRT rarely live longer than 4–5 years today, presumably as a result of the size-selective harvest, although that could change with management regulations. Our study also suggests that a stream resident population can become established fairly readily, given the creation of four age/size classes from a few small spawning events. Natural reproduction has been demonstrated to be possible repeatedly in the past few years, even when only small numbers of fish are allowed to spawn and when ripe adults have been transported to spawning areas (Moyle and Carmona-Catot 2009, unpublished data). The ability of large numbers of fish to make spawning migrations has still not been conclusively demonstrated although there is evidence it is possible (Pustejovsky 2007; Thompson et al. 2007). There is ample evidence that juvenile ELRT can persist and grow in small numbers even in the presence of dense populations of aggressive, predatory brook trout (Carmona-Catot et al. 2010). Brook trout, however, clearly present an obstacle to full recovery, while also demonstrating the capability of Pine Creek for supporting high densities of juvenile ELRT in the absence of brook trout.

Genetics

The lack of evidence for genetic bottlenecking in ELRT is encouraging for restoration. Records from the early hatchery program suggested that the small number of fish captured and spawned in the 1950s were the sole source of future populations (Moyle 2002). The genetic evidence now indicates that a residual population probably existed in the lake and spawned successfully on occasion, maintaining genetic diversity. Once all access to natural spawning was reduced (1959) then denied (1995), hatchery practices of spawning many females and using mainly progeny of 'wild' fish presumably maintained diversity. Nevertheless, some deliberate selection (for large size) and inadvertent selection (for early life history survival under hatchery conditions) no doubt have taken place. The rapid evolution of hatchery traits is well documented in salmonids and indicates the desirability of reestablishing natural spawning and rearing again as soon as possible (Heath et al. 2003).

Habitat

The alkalinity of Eagle Lake has made it remarkably resistant to invasions by non-native fishes and invertebrates that characterize other large California lakes (Moyle 2002). Its isolation at the edge of the Great Basin and frequently windy conditions have made it less desirable for recreation than nearby lakes (e.g., Lake Tahoe) and reservoirs (e.g., Almanor Reservoir), so it has been less settled by humans. In addition, large fluctuations in water levels and water chemistry have made it difficult to use its water for irrigation and other purposes. Increasingly, the lake is being recognized as important to protect for its native biodiversity, including large breeding populations of aquatic birds.

Pine Creek, the principal tributary, in contrast, is recovering from a century of damage from heavy grazing, logging, road and railroad building, and water diversion. The CRMP process has resulted in major improvements to the creek, including protection from cattle, improved culverts for passage, and other actions, and the improvements are still continuing. The creek remains perennial in its upper reaches thanks to several spring systems, with high quality spawning and rearing habitat (Pustejovsky 2007).

- **What changes in management of ELRT are required in order to re-establish a self-sustaining population in the Eagle Lake watershed?**

So far the focus of ELRT management has been to maximize the number of eggs taken to support hatchery operations and to plant large numbers of fish in the lake to sustain the trophy fishery. The ELRT management plan of DFG (Dean and Chapell 2005) indicates that the preferred option is to maintain the artificial propagation program but to continue cautiously with "efforts to restore a naturally spawning component in Pine Creek" (p 19). We agree that both elements need to be present, but from a conservation perspective a higher priority needs to be placed on restoring a self-sustaining population of ELRT than on providing large numbers of eggs for hatchery production, in part to replace artificial selection with natural selection. The need to establish a self-sustaining population after such as a long period of captive breeding is underscored by the findings of Chilcote et al. (2011). We see the changes in management required to bring this restoration about as simultaneously overcoming a series of obstacles, large and small: (1) brook trout dominance, (2) watershed damage, (3) hatchery demands, (4) management of the lake fishery, and (5) water diversions.

Brook trout dominance

In the late 1800s, brook trout were brought to California from eastern North America and were widely distributed around the state. They have been involved in the decline of many native trout species in California and the western USA (Moyle 2002). Brook trout were introduced into Pine Creek in 1940–1949 to provide a stream sport fishery. They were soon abundant in areas that ELRT used for spawning and rearing; today densities of brook trout average ca. 16,000 ha^{-1}, with local densities up to 30,000 ha^{-1}, which are among the highest recorded for California (Carmona-Catot 2009). It is likely that brook trout further suppressed the already diminished ELRT population through competition and perhaps predation on early life stages. Juvenile brook trout presumably dominated juvenile ELRT because they are larger in size, the result of earlier emergence times. Brook trout begin to spawn in October and the first newly emerged fry are observed in May; ELRT spawn from March to May, and fry are observed as early as June. In July 2009, brook trout fry averaged 50 mm (FL), 10 mm longer than ELRT fry (Carmona-Catot et al. 2010). Shepard et al. (2002) also found similar size effects between juvenile brook trout and westslope cutthroat trout (*Oncorhynchus clarki lewisi*). Not surprisingly, the presence of brook trout in spawning streams has discouraged efforts to re-establish natural runs of ELRT.

A treatment of Pine Creek with piscicides to remove brook trout has not been formally proposed because of the possibility of harming endemic invertebrates as well as legal and social difficulties (Moyle et al. 2008). Thus removal by electrofishing was evaluated in Bogard Spring Creek as an alternative to poisoning because it has minimal effects on nontarget species. Three years of electrofishing reduced the brook trout population to <1% of original numbers (Carmona-Catot et al. 2010), which can probably be maintained by the use of less invasive techniques, such as minnow traps (Moyle and Carmona-Catot, unpublished data, 2009) and a construction of a barrier. But this is at best a short-term solution confined to small spring-fed tributaries of the main creek, so ultimately eradication of brook trout using piscicides is likely to be needed.

Watershed damage

Numerous habitat improvements have been conducted within the watershed via the Pine Creek CRMP process. One of the main goals of the CRMP has been to improve habitat and access for ELRT, which has been quite successful. In 1995, the request to list ELRT under the Endangered Species Act (ESA) of 1973 was denied based partly on ongoing efforts to restore habitats within the Pine Creek watershed. Nevertheless, work still needs to be done, especially in relation to grazing, which impacts bank stability and riparian vegetation in places. In 2008 and 2009, the banks and bed of some headwater creek reaches were still damaged by cattle grazing, although others showed major recovery through reduction or exclusion of livestock grazing (G. Carmona-Catot and P. Moyle, pers. obs., 2008, 2009, 2010). The improvements to the Pine Creek watershed need to continue, with a focus on efforts that will improve summer flows and create refuges for ELRT (e.g., Bogard Spring Creek).

Hatchery demands

Today, although there has been considerable investment in improving conditions in the creek, as fish start to move upstream in the spring, a concrete weir completely blocks their migration as part of the egg taking station and does not allow any natural migration to the historical spawning grounds. For better or worse, a complex hatchery system has been developed around ELRT not only to intensively stock Eagle Lake for recreational fishing, but also many other waters in California (Fig. 2). The captive breeding program, with goal of saving the species in order to restore a successful fishery in Eagle Lake, has evolved into a production program which has inhibited action to restore wild populations, despite many years of restoration of habitat in Pine Creek.

Part of the failure in previous tracking studies of spawning fish has been the lack of availability of suitable spawners. Up until now, the ELRT hatchery egg quota had to be met before any spawners could be used for restoration purposes. Because exceptionally large numbers of ELRT migrants were captured at the Pine Creek trap in spring 2009, DFG obtained approximately six million of eggs from the run, twofold the normal hatchery quota (Table 2). Despite this, DFG only allowed 10 spawning females and 21 males to be used for restoration studies, when more than 4,000 (females and males) migrants were estimated to enter the trap in addition to the 200–300 fish observed downstream from the dam that never made it upstream (P. Divine, DFG, pers. comm., 2009). The concern seems to be that reducing take of eggs would reduce total numbers of trout available to support the lake fishery, as well as other hatchery-based planting programs (Dean and Chapell 2005). Overall, a major change in management emphasis is needed, with the focus shifting to restarting a self-sustaining wild population, in conjunction with a brook trout elimination program.

Management of the fishery in Eagle Lake

The fishery for ELRT in Eagle Lake is widely regarded as a management success because it has been sustained as a trophy fishery for 40+ years (Moyle et al. 1995; Moyle 2002; Dean and Chapell 2005). At present, the fishery, as well as an ELRT population in Eagle Lake, would not exist without hatchery production of trout. However, studies are lacking to demonstrate the relationships among fishery success, number of fish stocked in the lake, age and size at stocking, and carrying capacity of the lake at different water levels. It is quite possible that the fishery (and growth rates of individual trout) could be improved by stocking fewer, rather than more, fish, for example. Thus doing a study of the biology of fish in the lake in relation to management, especially hatchery practices, would likely benefit both the fish and the fishery.

Water diversion

In 2010, the elevation surface level of Eagle Lake was more than 3.5 m lower than in 1875. The elevation has naturally fluctuated due to variable annual precipitation but diversions have likely kept lake levels somewhat lower (Pustejovsky 2007). In 2010, the lake was only ca. 2 m higher than the lowest levels in the past 140 years (Lassen County Public Works Department, unpublished data, 2010). The Bly Tunnel is still a threat to the lake because it discharges about 1.5 cfs (0.034 cubic m/s) of water, through a 20 cm pipe in the plug into Willow Creek for downstream water right holders (Bureau of Land Management 2010). Most water apparently percolates into the tunnel from Eagle Lake because it is chemically similar to Eagle Lake water (Moyle et al. 1991). It is important to keep as much water in Eagle Lake as possible by shutting off flows through the Bly Tunnel; a long drought could make the alkalinity levels too high for survival of the endemic fishes, such as ELRT, especially if the refuge potential of Pine Creek is lower than it was historically.

In the Pine Creek watershed, Bogard Spring Creek, an important spawning and study stream (Carmona-Catot et al. 2010), is subject to diversion. In dry summers, it is an important source of water to Pine Creek downstream from the confluence (G. Carmona-Catot, pers. obs., 2007, 2008, 2009). Despite this, part of the spring flow of the creek is continuously being diverted to provide water for a rest stop facility on Highway 44 and for a USFS Work Station. Although data on water diverted is limited, the mean for 1996, 2000, and 2005 was ca. 35 m^3/day and it increased to almost 60 m^3/day in 2007 (USFS Lassen National Forest, unpublished data, 2010). Diversion seems to increase during the summer and early fall when water is most needed in the creeks for ELRT rearing and survival, suggesting that the elimination of this diversion is desirable.

Conclusions

ELRT present an unusual opportunity for restoration of a self-sustaining wild population of a distinctive subspecies of rainbow trout. Although management of ELRT has emphasized hatchery production for the past 60 years, the basic biological traits of the species still seem to be intact and it remains reasonably diverse genetically. Although management has apparently managed to minimize negative effects of hatchery rearing, reestablishing a wild population would ensure the maintenance of its distinctive life history and its value for future use as a hatchery fish (e.g., through avoidance of disease epidemics in hatcheries). An important factor that makes reestablishment possible is that the habitat in Eagle Lake is still intact and that Pine Creek, its major spawning stream, is recovering as habitat. With one exception, the habitat factors that led to the presumed near-extinction of ELRT in the early twentieth century have been ameliorated, although improvements are still needed. The one major exception is the large population of brook trout in key spawning and rearing areas.

The ELRT fits the definition of a threatened species under both state and federal Endangered Species Acts because it is in danger of extinction throughout its native range as a wild, self-sustaining species. It is entirely dependent on captive breeding for its survival, with all the inherent problems, such as disease epidemics in the hatcheries, selective breeding, and loss of funding to maintain hatchery programs. It is currently listed as a Species of Special Concern by DFG. The American Fisheries Society considers ELRT to be a threatened species and NatureServe has listed it as "critically imperiled" (Jelks et al. 2008). The National Marine Fisheries Service guidelines indicate that a salmonid population dependent on hatchery production cannot be considered as viable in the long term (McElhaney et al. 2000). If significant progress is made to re-establish a naturally-spawning population in the next 5 years, listing may not be needed. Indeed, rapid listing may reduce the ability of local agencies to accomplish restoration tasks quickly and efficiently without permitting delays. However, listing would dramatically underscore the need to connect habitat restoration with actual reestablishment of a wild population and provide additional incentives to deal with brook trout and other problems. It is worth noting that a threatened species designation would not preclude maintaining the fishery in Eagle Lake or elsewhere. Whether ELRT is listed or not, we recommend the following measures to assure the future of ELRT as a wild fish.

Brook trout

Without severe reduction or eradication of brook trout populations in Pine Creek, restoration of ELRT to a large self-sustaining population will be unlikely. We envision a four pronged process. (1) Maintain Bogard Spring Creek as an experimental spawning stream through control of brook trout by electrofishing, as demonstrated by Carmona-Catot et al. (2010), and through construction of a two-way weir (Carbine and Shetter 1943; Whalls et al. 1955) at the mouth of the creek to prevent recolonization by brook trout. (2) Allow and track spawning of adult ELRT in Pine Creek, to see if ELRT can establish at least a small population in the presence of brook trout. (3) Conduct surveys of aquatic invertebrates and amphibians to see if there are endemic species likely to be negatively affected by poisoning the stream with rotenone or other piscicides. (4) Conduct a brook trout eradication program, preferably in late summer of a dry year, using piscicides.

If the first two measures work, the last two may not be necessary. Reduction of non-native species, even when eradication is not reached, can allow native species to rebound to self-sustaining populations (Flick and Webster 1992). Given that brook trout became abundant in Pine Creek during years when ELRT were in severe decline due to limited access to spawning grounds from the lake, it is possible that with an intensive reintroduction program, ELRT could become the dominant species in Pine Creek, perhaps eventually eliminating brook trout through competition and predation as rainbow trout have done elsewhere (Kelly et al. 1980; Moore et al. 1983, 1986; Larson and Moore 1985; Fausch 1988). It is worth noting that some successful spawning and rearing occurred in Pine Creek before any brook trout removal had been conducted.

Continue stream improvements

We recommend reduction of livestock use of meadows even further by sensitive areas of Pine Creek and Bogard Spring Creek that are not already fenced, and by providing more off-creek watering stations within the watershed. Healthy meadows with stabilized banks and native riparian vegetation would make the creek more suitable for ELRT spawning and rearing (Purdy 2010). Climate change is likely to reduce snowpack in the mountains in the Pine Creek watershed (Maurer 2007; Cayan et al. 2008), which will presumably reduce spring outflows needed for spawning, and perhaps the output of springs that feed Pine Creek. The size of this effect, however, will depend on the timing of rainfall and how well meadows are managed to increase their ability to hold water and release it during the summer months.

Test passage improvements

Restoration actions have considerably improved access of ELRT to spawning habitat through removal of culverts and other barriers. Because Pine Creek is in significantly better condition today than it was in the past, restoration of a spawning run is increasingly possible and desirable (Pustejovsky 2007). There is still a need to determine if ELRT can pass through all the former barrier areas, so movements of radio-tagged mature fish from a natural run need to be studied.

Enhance flows

The diversion of water from the springs of Bogard Spring Creek to the USFS Work Station and rest area of Highway 44 should be eliminated to increase the flows of the creek. Water extraction continues while summer flows are very low and the creek could be essential for ELRT spawning and rearing. In addition, to help keep lake levels up water now being diverted through Bly Tunnel should shut off completely if possible. Groundwater extraction around the lake should also be evaluated and restricted if necessary.

Turn permanent weir to temporary barrier

Despite millions of dollars spent improving fish passage through the Pine Creek watershed (Pustejovsky 2007), the permanent dam at the egg taking station still remains and totally blocks the volitional migration of any trout to their historical spawning habitat. The barrier should be modified to allow free passage of ELRT and other native fish.

Assist migration to the upper watershed in dry years

There is still not total certainty that even if the weir at the mouth of the creek is modified, the fish will be able to migrate more than 45 km to the spawning habitat. To demonstrate the potential for assisted migration, 10 mature females and 11 males were captured at the Pine Creek weir and transported to the upper watershed in the spring of 2009 (Moyle and Carmona-Catot 2009, unpublished data). Spawning and rearing were successful, even though the only fish allowed to transported were very ripe and at the very end of the spawning season. These results indicate that trapping and trucking is a viable option for helping to recreate a naturally reproducing population in dry years when stream flows reaching the lake are not sufficient for migration.

Bogard Spring Creek as a experimental stream

Bogard Spring Creek is the only creek in the Pine Creek watershed where invasive brook trout have been controlled and densities reduced to low levels. Eradication of brook trout is thought to be possible if electrofishing removals are continued for a few more years, and immigration of brook trout from Pine Creek is prevented (Carmona-Catot et al. 2010). Given the success in controlling non-native brook trout in this once-important rainbow trout habitat, the development of Bogard Spring Creek into an experimental spawning stream would be a step forward in the reestablishment of a self-sustaining population of ELRT.

Conduct annual monitoring of Pine Creek

The management recommendations above are all experimental to some degree, so success will be best measured by annual monitoring in spring of spawning adults and in fall of juveniles (and of brook trout). Surveys performed in part by tribal members, anglers, and other citizens, under supervision of biologists, can also enhance community ‘buy-in’ of restoration efforts.

Development of a management plan

In order to tie all the management actions together, an integrated management plan is needed, that is flexible enough to be adapted to changing conditions. In particular, a genetic management plan should be part of the overall plan, to maximize the possibilities of enhancing genotypes and phenotypes for adapting to local conditions. A basic assumption of the management plan will be that both a hatchery based and wild spawning populations will be maintained, as mutual insurance policies.

Lessons for captive breeding programs of fishes

Captive breeding programs are considered successful when the imperiled species is re-established in the wild. They are usually regarded as a temporary strategy to maintain a species while habitats for reintroduction into the wild are being restored and self-sustaining populations are re-established (Anders 1998). Captive breeding programs are relatively new for most kinds of organisms, but salmonids have been reared in captivity for release into the wild for over 150 years, resulting in their becoming established in coldwater streams worldwide (Behnke 1992; Lever 1996; Crawford and Muir 2008). ELRT have been in reared in captivity for over 60 years resulting in the development of domesticated strains for use in put-and-grow fisheries, in the use of progeny of lake fish to support reservoir fisheries, and in the continuous release of captive bred individuals back into Eagle Lake. Domestication has resulted in ELRT that are well-adapted to hatchery rearing and that are widely planted in lakes and reservoirs but that rarely reproduce in the wild. Captive breeding has resulted in the wild-type ELRT that lives in its natural lake habitat and still appears to be able to complete its life history in the wild. Both domestic and wild types thrive only as long as hatchery programs are successful.

In one sense, the ELRT captive breeding program has been a major success because it has maintained a wild population large enough to be subject to considerable harvest. Although domesticated fish have been planted in the lake in the past (Moyle et al. 1995), most fish planted have been progeny of parents collected from the Pine Creek spawning run, with some care taken not to use any fish twice in the hatchery program. The result has been a captive population that has maintained much of its presumed historic genetic diversity through 60 generations of captive breeding. The lesson here is that a long-term captive breeding program can work if the animals are exposed to living in their native/natural environment for at least part of their life cycle and if genetic diversity is maintained in the captive population through large population size and genetic management.

However, the ELRT hatchery program also was fortunate that it was maintained without being shut down for disease outbreaks or lack of funds, as can happen to even the best run fish hatcheries. It is also likely that some selective breeding (e.g., for adult size, early maturation of eggs) was nevertheless taking place, even if inadvertently, that could reduce potential for reestablishing a wild population. Thus the apparent lack of observed negative impacts of captive breeding may simply reflect problems that take a long time to manifest themselves or requires more careful examination of the biology of the animals than had been done previously. Domestication selection caused by artificial spawning of captured adults could be further reduced by allowing for natural mate choice in the wild and collecting eggs a posteriori (e.g., Van Doornik et al. 2010). Rearing environment also can play a significant role in determining the phenotype and behavior of migratory species. Thus, in comparison to salmon reared in a traditional hatchery environment, salmon reared in a more natural setting have greater swimming endurance and predator-avoidance abilities, produce more eggs and more eggs surviving to hatch, and perform longer migrations (Chittenden et al. 2010). These biological traits are important for ELRT that will have to readapt its life cycle to the natural environment if it is ever released from total dependence on the hatchery program.

Another challenge faced by captive breeding programs is making sure the environment for reintroduction can actually sustain a wild population. It is clear from the history of ELRT and Pine Creek that restoring habitat can take decades and involve a dozens of actions of varying degrees of difficulty and cost. The restoration of Pine Creek has taken over 30 years already and some major actions still remain to make it fully habitable for ELRT, including eradication of brook trout.

We therefore see the following as some basic 'rules' of captive breeding of fish for release back into the wild:

1. Captive breeding programs should only be considered when other options have been exhausted and a species or population is faced with extinction.
2. Captive breeding should be a temporary measure while habitat or other limiting factors are being fixed, although 'temporary' may mean multiple decades.
3. The establishment of self-sustaining populations in the historical range should be the first priority for the program.
4. A genetic management plan should be in place in order to not lose genetic diversity and avoid inbreeding depression.
5. A captive breeding facility should make the rearing environment as natural as possible to reduce effects of selection by the hatchery environment.
6. Habitat restoration/protection has to be an integral part of any captive breeding program if the species is to truly persist as anything but a simulacrum of the wild form.

ELRT captive breeding program is unusual, perhaps unique, in its success at maintaining the apparent fitness of the species for survival in the wild over a long period; such fitness is usually greatly diminished in captive-bred salmonids in a few generations (Fraser 2008). The ability of ELRT to complete its entire life cycle successfully is still an open question but the indicators so far are good, provided there is no delay in instituting a program that allows life cycle restoration to happen on an increasingly large scale. The probability of restoration success is enhanced by the fact the entire Eagle Lake watershed is in good condition compared to so many other watersheds in the state; it fits well with the visionary concept of Native Fish Watersheds as a key for aquatic conservation (Williams et al. 2011). At the same time, as is the case with large scale conservation plans in general, three major factors work against their achievement: conflicting human uses of the land, water, and biota, climate change, and non-native species. The challenges facing ELRT such as demand for their use as hatchery fish, use of the riparian lands for grazing, out-of-basin use of water, and competition from brook trout, all have to be resolved in an environment that is changing rapidly. Extinction is always an option and it becomes increasingly likely if we fail to act boldly.

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