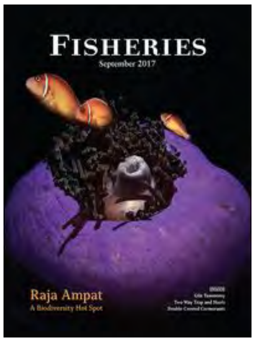

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Robert A. Lusardi & Peter B. Moyle

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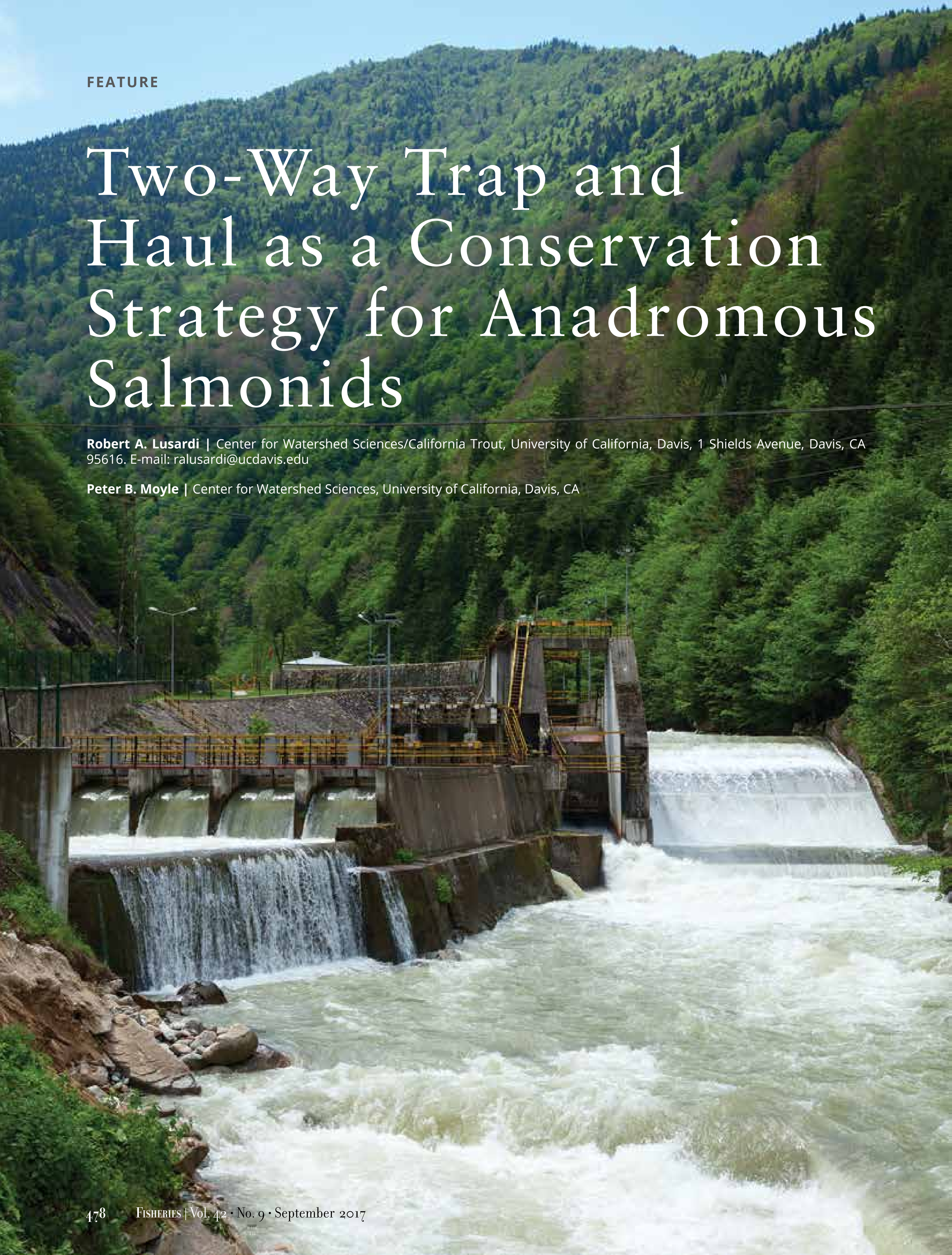
FEATURE

Two-Way Trap and Haul as a Conservation Strategy for Anadromous Salmonids

Robert A. Lusardi | Center for Watershed Sciences/California Trout, University of California, Davis, 1 Shields Avenue, Davis, CA 95616. E-mail: ralusardi@ucdavis.edu

Peter B. Moyle | Center for Watershed Sciences, University of California, Davis, CA



Dams are ubiquitous in the United States and have disconnected migratory fishes from important historical habitat. Trapping fish and moving them around dams (trap and haul) is a common strategy to manage Pacific coast salmonids. Usually, juveniles or adults are moved in one direction, but there is growing interest in two-way trap and haul (TH2), where both adults and out-migrating juveniles are captured and transported over dams. Despite recent technological advances, no TH2 program is an unequivocal success. Our review indicates that uncertainties associated with TH2 programs exist and include delayed effects from transportation, maintenance of above-dam populations, out-migrant capture efficiency, and the role of hatchery supplementation. Two-way trap and haul programs should (1) clearly define measurable and objective success metrics, such as the 10 we provide; (2) proceed experimentally under an adaptive management framework to determine risk–benefit trade-offs; and (3) be part of comprehensive conservation strategies that consider the entire life cycle of each species. Two-way trap and haul is proposed as a high-priority recovery strategy for Chinook Salmon *Oncorhynchus tshawytscha* populations in California. Our findings indicate that any such TH2 program should proceed with extreme caution.

INTRODUCTION

Dams are pervasive in the United States and have disconnected migratory fishes from important historical habitats, causing declines in many species. Getting fish over dams has been a major challenge, resulting in creation of diverse passage devices, such as fish ladders and elevators. Many dams, however, are too high to support volitional passage of fish; they also create extensive reservoirs, which present formidable barriers for passage. When volitional passage is not feasible, three alternatives are generally considered for sustaining migratory fish populations: (1) abandon the goal of sustaining migratory fish populations, (2) use below-dam hatcheries to replace the historical contribution of upstream habitats to migratory fish populations, and (3) increase or improve habitat in rivers below dams. All of these methods have their drawbacks and generally result in a decline of migratory fish in watersheds dominated by large dams (Montgomery 2003; Lackey et al. 2006). This is especially true in California, where most rivers have dams that block fish passage to upstream areas (Yoshiyama et al. 2001; Hanak et al. 2011).

Increasingly, solutions that provide wild fish access to rivers above impassable dams involve either dam removal (Quiñones et al. 2015) or capturing fish and moving them above dams by truck or other means, as part of a reintroduction program. Such reintroduction programs are generally labeled as trap and haul (TH). Two-way trap and haul (TH2) occurs when both adults migrating upstream and juveniles moving downstream are trapped and moved around a dam. This type of program is currently under consideration to sustain Chinook Salmon *Oncorhynchus tshawytscha* (hereafter, Chinook) runs in California, which are threatened with extinction. However, there may be uncertainty regarding the efficacy of such programs (Anderson et al. 2014). We (1) provide a general review of TH operations as a conservation tool, especially use of TH2; (2) examine existing programs in the Pacific Northwest; (3) present some general guidelines for TH2 operations; and (4) discuss the proposed use of TH2 for improving the conservation status of Chinook in central California.

TRAP AND HAUL: A REVIEW

There is a long history of moving fishes to new locations by truck, train, or ship (George et al. 2009). Indeed, the success of this process has resulted in some species being spread worldwide, especially salmonids. TH also has a long history (George et al. 2009; IUCN Species Survival Commission 2013) and is gaining increased attention as assisted migration to counter the effects of climate change (McLachlan et al. 2007). However, most of this movement of fishes has involved transporting small individuals, usually juveniles or embryos, to new locations. In recent years, it has become fairly common to move either adult or juvenile salmonids to maintain existing populations (DeHaan and Bernall 2013; Sigourney et al. 2015). Movement is typically over human-made barriers, from dams to dry riverbeds. For example, in the Columbia River, millions of juvenile Chinook and steelhead *O. mykiss* are trapped in upstream areas and moved by barge for release in the lower river (Montgomery 2003). The following are brief summaries of literature dealing with TH for juvenile and adult salmonids, recognizing that TH is also employed for other fishes such as Pacific Lamprey *Entosphenus tridentatus* (Corbett et al. 2014) and European Eel *Anguilla anguilla* (J. Geist, Technische Universität München, personal communication).

Juvenile Salmonid Trap and Haul

Most studies on TH of juvenile salmonids have occurred in the Columbia River system, where barges have been used to transport fish for decades. They show that success of TH varies by transport timing, distance, target species, fish density, stress, and delayed effects (Congleton et al. 2000). For example, downstream transport of juvenile Chinook is most successful when barges carry individuals long distances, as opposed to trucks (Ward et al. 1997; McMichael et al. 2011). Stress from trucking apparently makes small salmon more vulnerable to predation after release, while transport via barge may condition fish to avoid predation and reduce disease susceptibility (Arkoosh et al. 2006). Stress from TH is cumulative (handling + transportation) and may reduce disease resistance, swimming ability, and osmoregulatory ability (Maule et al. 1988). However, juveniles of some species (Chinook vs. steelhead; Congleton et al. 2000) and runs (fall vs. spring Chinook; Maule et al. 1988) are apparently more sensitive to TH than others. Timing of transport may also be particularly important, with late-season low flows contributing to poor water quality during transport and reduction of survival of certain species (Clemens et al. 2009).

Increased juvenile survival, through stress reduction, is crucial for long-term success of TH. Conditioning of juveniles prior to transport, through exposure of changing water levels coupled with feeding, may reduce stress (Schreck et al. 1995). Positive effects from conditioning may include improved osmoregulation, disease resistance, and survival. When river conditions are stressful, such as during periods of low flow, survival of transported fish may be higher than that of nonassisted counterparts (Ebel et al. 1973; Holsman et al. 2012).

Delayed transport effects on juvenile salmon, however, are well documented (Budy et al. 2002). Barge transport has been shown to impair juvenile salmonid auditory function (Halvorsen et al. 2009), which may compromise predator avoidance adaptations. Barge-transported smolts may experience earlier ocean entry and reduced growth rates, leading to enhanced mortality from predation (Muir et al. 2006; Rechisky et al. 2012). Juvenile transportation may also decrease the homing ability of adults. Chapman et al. (1997) found that transported juvenile out-migrants were more likely to have impaired homing behavior as adults. Bond et al. (2017) found that Columbia River transported juveniles were up to 19 times more likely to stray as returning adults than in-river migrants. Similarly, Keefer et al. (2008) found that Columbia River salmonids subjected to barge transportation as juveniles strayed more often as adults than in-river migrants and were also more likely to experience adult failure to pass dams.

Overall, these studies indicate that TH of juveniles works only if great care is taken in capture and handling before, during, and after transport. They also suggest that juvenile salmonids released after transport experience delayed mortality and thereby contribute little to adult returns. It is worth noting that TH of juvenile salmonids is typically with hatchery-reared fish.

Adult Salmonid Trap and Haul

TH of adult salmonids is much less studied than that of juveniles. However, it has been used successfully in places where water is cold and transport distance is short. For example, since 1958 thousands of adult Sockeye Salmon *O. nerka* have been trucked each year over Sunset Falls on the south fork of the Skykomish River in western Washington to provide access to 145 km of habitat (Aurdahl et al. 2001). Juveniles move downstream naturally. More recently, Sigourney et al. (2015) found that adult TH of Atlantic Salmon *Salmo salar* on the Penobscot River improved migration success to headwater spawning tributaries compared to salmon that navigated passage over three dams in the lower watershed.

Adult TH has also been recently used for spring-run Chinook in the Willamette River basin, Oregon. Using genetic parentage analysis, Evans et al. (2016) found that TH hatchery pairs were less fit than their wild counterparts and that the female cohort replacement rate (CRR; the number of returning adults produced by each reintroduced individual) ranged between 0.96 and 1.56 over 3 years of study. A CRR greater than 1.0 suggests population replacement and demographic stability without the influence of immigration. In another adult TH program, Sard et al. (2016a) found that female CRRs were 0.31–0.40 over 2 years of study, indicating insufficient population replacement. Adult sex may play an important role in sustaining populations of TH species. Both Evans et al. (2016) and Sard et al. (2016b) used female CRR because populations were male skewed, indicating that male reproductive opportunities were limited by number of females. In another Willamette basin TH program, O’Malley et al. (2015) found a female CRR of 1.07. However, when all out-planted individuals were taken into consideration, the CRR decreased to 0.54. The results collectively suggest that there is high uncertainty associated with the ability of adult TH programs to meet population replacement goals.

Movement of adults may also have consequences. Keefer et al. (2010) found that spring-run Chinook adults, on average, experienced 48% prespawn mortality when planted above dams on the Willamette River and that mortality was most strongly correlated with body condition and sex, as well as time of transport. When stressed adult spring-run Chinook were moved a short distance upstream in Butte Creek, California, after capture by nets and transportation by truck, they suffered 100% mortality (Mosser et al. 2013). After transporting small numbers of adult Westslope Cutthroat Trout *O. clarkii lewisi* and Bull Trout *Salvelinus confluentus* over a dam, Schmetterling (2003) found that while many continued upstream to spawn, pre- or postspawn mortality was common and associated with predation, harvest, failure to successfully pass dams, or movement into unfavorable habitats. Adult TH has also been used on the Toutle River, Washington, where steelhead and Coho Salmon *O. kisutch* have been annually transported by truck since 1989 to upstream tributaries. Telemetry studies showed that most recently transported Coho Salmon remained close to the release site and about 20% died (Liedtke et al. 2013).

Two-Way Trap and Haul

When volitional passage over large dams, both upstream and downstream, is not deemed possible, TH2 is used to reestablish migratory fish populations above barriers. TH2 involves capturing adult fish below the dam and transporting them to a release site above the dam. Adults must then spawn successfully, producing large numbers of fish that can be captured and transported for release below the dam. These juveniles then continue to rear in the release area or migrate downstream, eventually to the ocean.

Moving both adult and juvenile salmon over barriers is done on a regular basis in a number of river systems (Table 1). Aurdahl et al. (2001) discussed, from an engineering perspective, a wide variety of options for TH2 of salmonids over three hydropower dams on the Snake River, balancing cost and effectiveness. They concluded that trapping adults below the lowest dam and releasing them above the upper dam can be successful with carefully designed trucks and other facilities. However, capturing large numbers of out-migrating juveniles was a larger challenge, requiring traps in reservoirs.

Fish attraction barges (gulpers) have been used for decades to trap juvenile Sockeye Salmon moving into lower Baker Reservoir on the Baker River in Washington, with the design modified a number of times to improve success (Aurdahl et al. 2001). Many gulpers have been upgraded to floating surface collectors (FSC) to improve capture of out-migrant salmonids (Figure 1). Floating surface collectors use an attraction flow and nets to guide out-migrants into a narrow channel, through a series of gates. The fish eventually end up in a raceway, where they are crowded into a transport hopper and moved to an evaluation station. Individuals are then transferred to tanks and are ferried to transport trucks, which move juveniles to “stress-relief” ponds for up to 48 h before release below the dam (D. Bruland, Puget Sound Energy, personal communication).

The Baker River TH program was established in 1925 with completion of Lower Baker Dam. The program initially focused on only trapping adult salmon and moving them above the dam to the upper watershed. With the construction of Upper Baker Dam in 1959, the program began using gulpers on both the lower (1958) and upper (1960) Baker reservoirs to assist in capture and transport of juvenile salmonids downstream to the Skagit River. More recently, precipitated by a strong decline in adult Sockeye Salmon returns, both gulpers were upgraded to FSCs (PSE 2015a, 2015b) and hatchery facilities were improved to increase fry production. Currently, FSCs are used in both the upper (since 2008) and lower (since 2013) Baker reservoirs. The technology is also being used on Swift Reservoir (Lewis River) and Cushman Reservoir (North Fork Skokomish River) in Washington (Table 1).

On the Baker River, hatchery upgrades and construction of two FSCs have enabled large increases in capture of Sockeye Salmon fry and smolts for eventual transport and release downstream. The timing of these upgrades is strongly associated with an increase in adult returns to the Baker River. Between 1980 and 2008, before facility upgrades, adult returns averaged approximately 5,000 adults per year. However, following the improvement of facilities, adult returns increased on average to 30,000 fish annually, with an all-time peak return of 50,177 in 2015 (Fig-

Table 1. Examples of two-way trap and haul (TH2) programs used in watersheds with high-head dams (>30 m) in North America.

				Collection facility location			
River	Tributary to	Adult	Juvenile	Dam owner	Target species	Juvenile collection method	TH2 completion date
Lewis	Columbia River	Merwin Dam	Swift Reservoir	PC	SRC, CO, SH	Floating surface collector	2012
Cowlitz	Columbia River	Barrier Dam	Cowlitz Falls Dam	TP and LCPUD	SRC, CO, SH, CCT	Fixed surface flume collector	1996. Capture efficiency upgrades in 2017.
Baker	Skagit River	Lower Baker Dam	Upper Baker and Shannon Reservoirs	PSE	SO, CO	Floating surface collectors	2008, 2013
Deschutes	Columbia River	Pelton Reregulation Dam	Lake Billy Chinook	PGE and CTWSRO	SRC, SO, SH	Selective water withdrawal tower	2009
North Fork Skokomish	Skokomish River	Cushman Dam No. 2	Cushman Reservoir	TP	SRC, CO, SH, SO	Floating surface collector	2014. Evaluation period.
South Fork McKenzie	McKenzie River	Cougar Dam	Cougar Reservoir	USACE	SRC, BT	Portable floating fish collector	2013. Experimental. Final design by ~2020.

Note. Dam owner abbreviations: PacifiCorp (PC), Tacoma Power (TP), Lewis County Public Utility District (LCPUD), Pacific Sound Energy (PSE), Portland General Electric (PGE), Confederated Tribes of the Warm Springs Reservation of Oregon (CTWSRO), U.S. Army Corps of Engineers (USACE). Species abbreviations: spring-run Chinook Salmon (SRC), Coho Salmon (CO), steelhead (SH), fall-run Chinook Salmon (FRC), Sockeye Salmon (SO), Coastal Cutthroat Trout (CCT), Bull Trout (BT).

ure 2). The relative importance of increased hatchery supplementation and addition of FSCs with respect to adult abundance cannot be readily distinguished. Strong positive relationships exist, however, between the number of hatchery fry released and total out-migrants captured (Figure 3), indicating that supplementing reintroduced stocks with hatchery individuals increased capture between 1996 and 2014. The number of returning adults was also highly correlated with total hatchery fry released (Figure 4), suggesting that hatchery supplementation of juveniles plays an important, perhaps dominant, role in the number of returning adults.

In 2009, a TH2 program was implemented on Deschutes River, Oregon, to provide access to spawning and rearing habitat above three dams. Returning adult spring-run Chinook, steelhead, and Sockeye Salmon are captured below Pelton Dam and trucked upstream above Round Butte Dam, where they are released. Out-migrating juveniles are attracted by flow and temperature cues provided by a water withdrawal tower constructed near the Round Butte Dam spillway. Here, individuals are sorted by species, tagged, and trucked downstream for release into the lower Deschutes River. Between 2010 and 2014, as part of a supplementation program, more than 5.8 million hatchery fry and smolts of spring-run Chinook and steelhead were released into tributaries above Lake Billy Chinook Reservoir. Approximately 169,000 (3%) of these fish migrated through the reservoir and were captured at the juvenile out-migrant trap. Depending on year and species, juvenile out-migration capture rates varied from 0.3% to 7.9% (Table 2). Between 2011 and 2014, a total of 102 and 337 adult spring-run Chinook and steelhead, respectively, returned to the Pelton adult trap. While the specific mechanisms for juvenile mortality have not yet been isolated, researchers suggest that low smolt to adult returns may be due to delayed mortality associated with either reservoir pathogens or handling stress of juveniles (PGE and the Confederated Tribes of the Warms Springs Reservation of Oregon 2015).

TH2 operations are also being used on adfluvial populations of Bull Trout. On the Clark Fork in Montana, adults are trucked to upstream natal tributaries to spawn above dams and out-migrating juveniles are trapped and transported downstream to Lake Pend Oreille to take advantage of productive rearing habitat (Al-Chokhachy et al. 2015). Strict genetic protocols are used to assign individual adult fish to natal tributaries. DeHaan and Bernall (2013) found that this program led to successful spawning and increased genetic diversity of populations above barriers. However, Al-Chokhachy et al. (2015) modeled effects of adult removal on donor Bull Trout populations and found that risks to donor populations increased with age of fish removed and total fish removed; their models also suggested that decline of the donor population under a trap and haul program was apparent even when adult return rates were exceptionally high (>12%).

The only attempt so far to develop a TH2 program in California has been in the lower San Joaquin River. Reestablishment of spring-run Chinook is legally mandated, after their extirpation 65-plus years ago (Börk et al. 2012). In 2013, fall-run Chinook were used in an experimental program to test TH2 success. Adults were captured in the lower San Joaquin River and ditches into which they strayed. Individuals were trucked upstream and released into the river (D. Portz, U.S. Bureau of Reclamation, personal communication). Over a 2.5-month period, 367 adult salmon were translocated, and many (30%–50%) were able to successfully spawn. Additional fish were spawned artificially and juveniles reared in in-river enclosures. Out-migrating juveniles were captured in March and April in the spawning reach using a variety of techniques, including weirs that spanned most of the river. About 1,100 juveniles were captured and successfully released approximately 160 km downstream. It was estimated that these juveniles would produce somewhere between 1 and 23 adults (Portz, personal communication).

A key question in any TH2 program is, How many fish need to be transported to make a program sustainable? A TH2 program can be deemed a success only if it produces enough adults to sustain the program or provide a surplus (i.e., CRR > 1.0). Determination of CRR using genetic parentage analysis should be a primary success metric of any experimental TH2 program (e.g., Evans et al. 2016; Sard et al. 2016b). For programs under consideration, life cycle models addressing population replacement should be developed in order to understand costs and benefits associated with a program. The model should ideally contain estimates of (1) adult fecundity and embryo survival; (2) juvenile survival above the dam; (3) juvenile capture rates; (4) juvenile mortality due to transport, including postrelease mortality; (5) mortality rates of

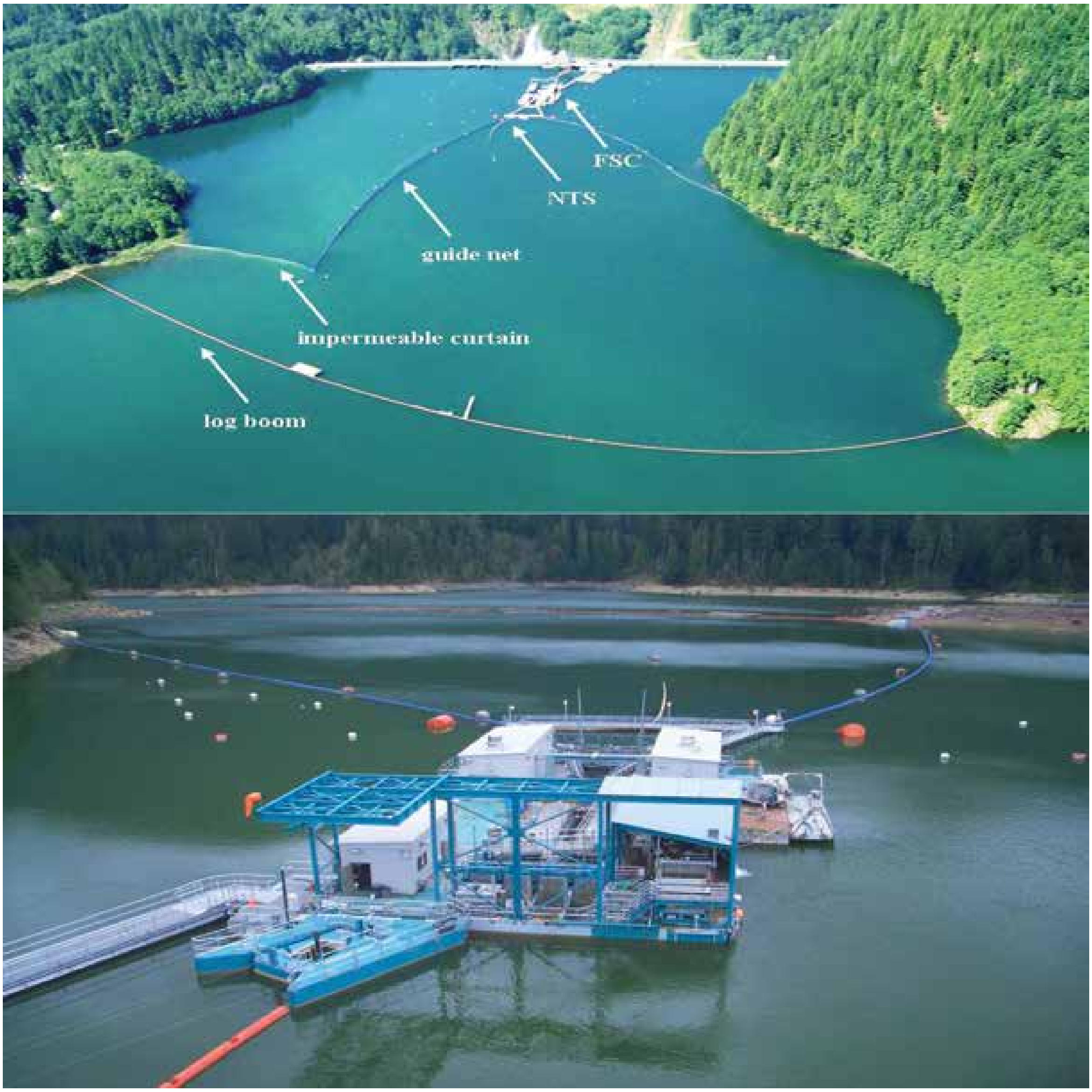


Figure 1. Floating surface collector used to capture out-migrating juvenile Sockeye Salmon on the upper Baker Reservoir (aerial looking down reservoir [top] and looking up reservoir [bottom]). Captured juveniles are transported by truck downstream and released below dams once processed through the floating surface collector. FSC = floating surface collector; NTS = net transition structure. Photo credit: Puget Sound Energy.

Table 2. Total juveniles released above Lake Billy Chinook Reservoir, captured at the out-migrant trap at Round Butte Dam, and total adult returns at the Pelton Dam adult trap between 2010 and 2014.

	Total fry and smolt released		Total juveniles captured		% juvenile out-migrants captured		Total SRC and SH adult returns	
Year	SRC	SH	SRC	SH	SRC	SH	SRC	SH
2010	546,488	625,137	43,438	7,612	7.9	1.2	—	—
2011	572,084	719,590	30,641	10,452	5.4	1.5	7	32
2012	503,189	621,122	24,236	7,806	4.8	1.3	48	128
2013	611,214	629,510	20,913	2,705	3.4	0.4	22	96
2014	278,718	715,235	18,662	2,113	6.7	0.3	24	81
Total	2,511,693	3,310,594	137,890	30,688	5.5	0.9	102	337

Note. The two-way trap and haul reintroduction program was first implemented in December 2009. Data source: Federal Energy Regulatory Commission, Pelton Round Butte Hydroelectric Project (Project No. 2030). Species abbreviations: spring-run Chinook Salmon (SRC), steelhead (SH).

juveniles/smolts migrating downstream to the ocean; (6) ocean mortality/survival rates; (7) adult mortality, including from fishing; and (8) adult mortality from capture stress. A sensitivity analysis could determine which rates are most important for determining number of returning adults.

One model that gives some idea of the adult numbers necessary for a successful TH2 program can be found in the recovery plan for winter-run Chinook in the Sacramento River, California (Lindley and Mohr 2003). The model indicates that a population of fewer than 100 adult females each year would likely go extinct. At least 10,000 females are needed for recovery (i.e., a self-sustaining population with low probability of extinction). Assuming a 1:1 sex ratio, these levels would result in minimum population estimates of 200 (quasi-extinction) and 20,000 (recovery; Lindley and Mohr 2003). This suggests that several thousand adults would ultimately be needed annually for TH2 in order to achieve recovery, along with hundreds of thousands of juveniles captured and returned to the Sacramento River. Given sufficient resources, such a program may be possible for salmon and steelhead in some rivers in central California, although much would depend on juvenile capture efficiency and whether existing populations of salmon and steelhead below dams can sustain having large numbers of adults removed each year for TH2.

Numbers transported may be much lower if the main goal is to create population redundancy. Genetic considerations are especially important in this situation (Meek et al. 2014). As few as 24 to 100 fish per year may be sufficient to protect against loss of genetic diversity over the short term (<10 years; Eldridge et al. 2009 and references therein), given strict mating and release guidelines (Fraser 2008 and references therein) and high juvenile survival. But even here, estimated target numbers for a genetically diverse population are necessary to determine program success.

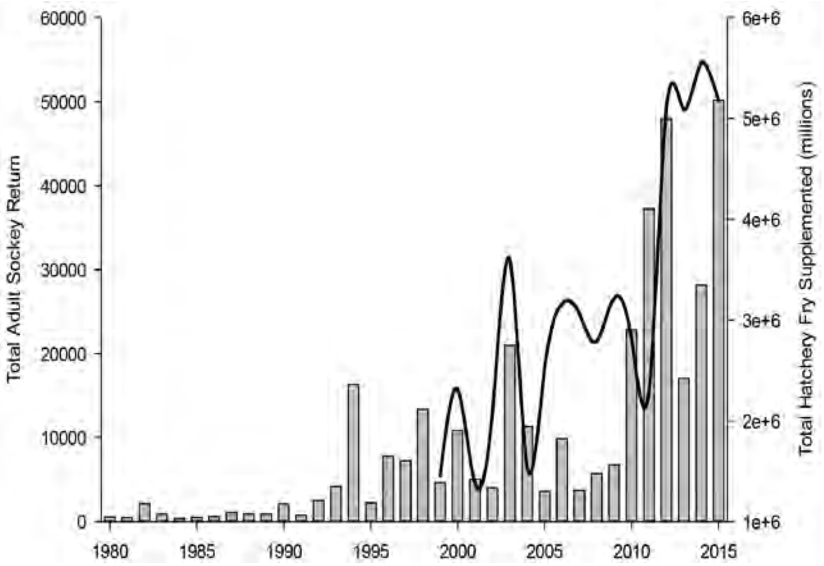


Figure 2. Adult Sockeye Salmon returns (bars) and total hatchery fry releases on the Baker River (line). Floating surface collectors replaced traditional gulpers in the upper Baker Reservoir and lower Baker Reservoir in 2008 and 2013, respectively. Fry released were offset by 3 years to account for adult ocean residency. Data source: Doug Bruland, Puget Sound Energy.

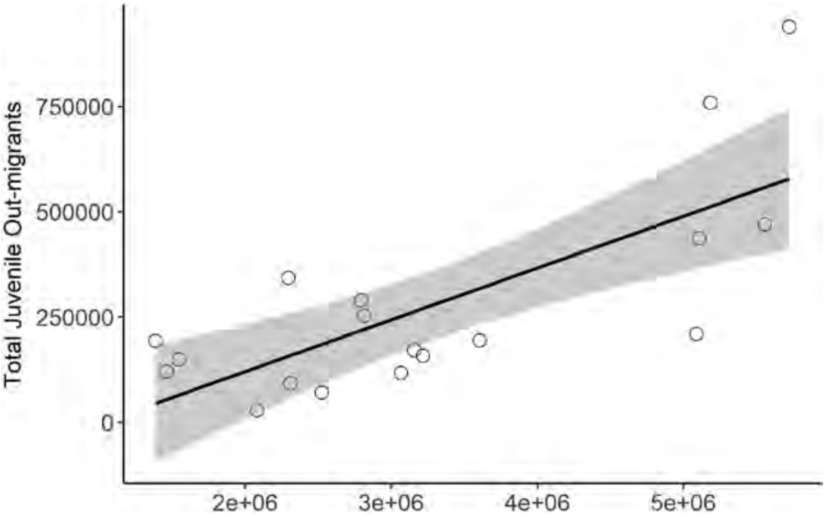


Figure 3. Total juvenile out-migrant Sockeye Salmon captured as a function of total hatchery fry released into the upper and lower Baker reservoirs between 1996 and 2014 ($r^2 = .52$, $P < .001$). Shaded region is the 95% confidence interval of mean predictions. Out-migrant data were offset by 1 year to account for juvenile rearing. Data source: Doug Bruland, Puget Sound Energy.

Two-Way Trap and Haul and Reintroduction Considerations

TH2 operations assume that the ecosystems into which fish are moved will support introduced fish, although several salmonid translocation programs have failed because of inadequate habitat in recipient areas (Harig et al. 2000; Harig and Fausch 2002). This assumption has to be carefully tested in TH2 programs. A stream above a dam that has been long deprived of its annual influx of nutrients from spawning salmon will likely be much less rich in invertebrates and other food needed to support large numbers of juvenile salmon than it was historically, based on studies of streams with and without spawning salmon (see Quinn 2005). Resident fish may also prey on or compete with reintroduced fish (Ward et al. 2008), although some studies have shown limited or no such interactions (Naman et al. 2014). A particular problem is piscivorous fishes resident in downstream reservoirs, which will prey on out-migrating juveniles from TH2 programs both in the reservoirs and in streams (Sanderson et al. 2009). In many reservoirs, Chinook and other migratory salmonids have established apparently self-sustaining populations as the result of stocking hatchery fish (Romer and Monzyk 2014; Perales et al. 2015). Reservoir populations of steelhead that spawn in tributary streams are fairly common in California (Moyle 2002). This suggests that adfluvial and TH2 salmonids are likely to interact and possibly interbreed (Sard et al. 2016a). In addition, transported fish may introduce pathogens into the recipient environment or may become infected with pathogens already present (Anderson et al. 2014).

There are also potential genetic considerations stemming from reestablishment of adult populations above dams. On one hand, population redundancy can reduce extinction risk associated with stochastic processes, improve interpopulation genetic diversity, and increase effective population size (Lusardi et al. 2015). This may especially be true where a species has been reduced to one population, as is the case with winter-run Chinook in California. However, these benefits are highly dependent on the condition of the source population and, further, assume that there are minimal effects to donor populations associated with removal of individuals. In cases where TH2 is used as a rescue strategy for endangered species, removal of individuals from extant wild populations may not be possible, and captive breeding programs would therefore be required. However, hatchery-reared individuals may exhibit reduced genetic diversity, lack potential to adapt to new or changing environments, and retain traits that are maladapted to natural environments (Araki et al. 2007; Chilcote et al. 2011; Christie et al. 2012). Reductions in fitness through outbreeding depression may also be considerable where strong differences in environmental selection pressure exist between donor and recipient habitats (Weeks et al. 2011).

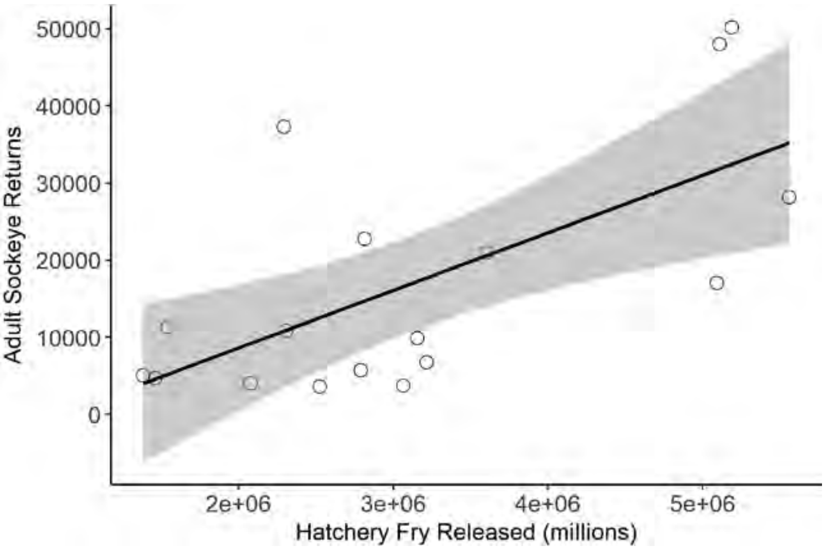


Figure 4. Total adult Sockeye Salmon returns in the Baker River watershed as a function of total hatchery fry released into the upper and lower Baker reservoirs prior to out-migration capture between 1999 and 2013 ($r^2 = .39$, $P < .01$). Shaded region is the 95% confidence interval of mean predictions. Fry released were offset by 3 years to account for juvenile rearing and adult ocean residency. Data source: Doug Bruland, Puget Sound Energy.

REQUIREMENTS FOR A SUCCESSFUL TWO-WAY TRAP AND HAUL PROGRAM

TH2 programs focus on improving salmon survival during critical components of their life histories. Passage above dams to historical spawning and rearing habitat and efficient capture of out-migrant juveniles can, in theory, provide numerous population benefits, most of which are realized through improved population structure and abundance. However, our review of the literature and data indicates that there are numerous uncertainties associated with TH2 programs and that no program can be declared an unequivocal success. Such uncertainties include delayed effects associated with transportation, maintaining population replacement and demographic stability, juvenile capture efficiency, and the role of hatchery supplementation. In addition, there are risks associated with reintroductions of salmonids into historical habitat. Complicating matters, the majority of TH2 programs for high dams (>30 m) in the Pacific Northwest either were very recently implemented or are currently functioning in an experimental capacity (Table 1), and there is a lack of long-term success associated with such programs. Despite the uncertainties associated with TH2, there may be individual cases where exploratory use of such programs is justified. Such situations exist where a species is critically endangered, lacks sufficient spatial diversity and population redundancy, or exhibits diminishing population replacement. In such cases, we strongly recommend that any TH2 program have the following characteristics:

1. There is a clearly defined success metric, with goals set in numerical terms and related to the number of returning adults that are progeny of previous TH2 spawners. Population replacement rates should be greater than 1.0 and monitored using genetic parentage analysis in exploratory programs or modeled for programs under consideration. An exception can be made if the donor population is threatened by imminent extinction if no action is taken.
2. There is adequate spawning, incubation, and rearing habitat in the recipient river to meet success metrics. Suitable water temperature is regarded as a key part of this assessment.
3. The effects of climate warming on stream temperatures and hydrological processes at potential reintroduction sites will not affect program success.
4. Captive breeding facilities used in conjunction with translocation programs, such as salmon hatcheries, are operated with established genetic protocols to increase survival of progeny in the wild and decrease artificial selection.
5. Trapping and transport of adults and juveniles between donor and recipient rivers minimizes stress and potential for delayed mortality.
6. Traps for collecting juveniles from the recipient river are effective in capturing sufficient juveniles to sustain a program.
7. A well-designed release program for juveniles back into river of origin is in place. This program must provide assurances that juveniles will have survival rates high enough to support an adult population at least as large as the number of adults moved originally into the recipient river.
8. Potential conflicts between existing runs of salmon (above dam adfluvial populations) and other fishes in recipient habitats are well understood to ensure that hybridization or competition for habitat is minimized.
9. The TH2 program is first conducted experimentally in an adaptive management framework where monitoring is in place in both donor and recipient rivers. Such an experimental program should use fish of known identity to determine success over the entire life cycle of the species. Experimental evaluations should also focus on effectiveness of out-migration capture independent of hatchery supplementation.
10. A TH2 program should be part of a more comprehensive program that considers all limiting factors on different life stages of the target species. Programs should not move independently of important restoration actions that improve,

for instance, downstream rearing habitat, migration routes to the ocean, or removal of dams to historically important tributaries.

In addition, guidelines for public outreach, stakeholder involvement, and communication of results should be incorporated into the program, as recommended by George et al. (2009). Transparency and stakeholder involvement is of the utmost importance. More general guidelines for conservation translocations and reintroductions can be found in IUCN Species Survival Commission (2013), Dunham et al. (2011), and Anderson et al. (2014). These guidelines are particularly useful for making decisions as to whether or not a conservation translocation program is justified.

TWO-WAY TRAP AND HAUL AND CENTRAL VALLEY SALMONIDS

California supports the southernmost populations of anadromous fishes on the Pacific coast (Moyle 2002). The Central Valley (Sacramento–San Joaquin) watershed alone once supported runs of 1–2 million adult Chinook per year, divided into four distinct runs (fall, late fall, winter, and spring; Yoshiyama et al. 2001). More than 70% of the historical spawning and rearing habitat for these salmon was in rivers now above large dams; much of the best habitat has been drowned by reservoirs (Yoshiyama et al. 2001). For spring-run Chinook, the percentage of lost habitat is around 90%; it is 100% for winter-run Chinook. Below dams, these runs continue to decline as result of altered flows, degraded habitat, and a reliance on hatcheries to sustain populations (Katz et al. 2013). Consequently, winter- and spring-run Chinook are federally listed as endangered and threatened, respectively (Moyle et al. 2017).

In 2009, the National Marine Fisheries Service (NMFS) determined that the operation of federal and state water projects in the Central Valley are likely to jeopardize continued existence of winter-run and spring-run Chinook. Given the importance of large dams to the California economy, fish movement to historical habitat above dams has been put forward as a preferred alternative to dam removal, mainly through TH2. While NMFS has indicated that TH2 could potentially be applied to all major dams on anadromous fish streams, their initial focus has been on returning winter-run Chinook to the McCloud River above Shasta Dam and spring-run Chinook to the North Yuba River above two large dams (NMFS 2014).

The decline of winter-run Chinook in California has been exacerbated by recent drought. The only remaining population spawns below Keswick Dam, a small hydropower dam below Shasta Dam, from which cold water is released during summer for egg incubation and juvenile rearing. Due to diminished cold-water reserves, however, the wild population experienced nearly 100% mortality in 2014 and 2015 and the unique run is on the brink of extinction. Recovery options for winter-run Chinook are extremely limited. Dam removal or other means of volitional passage are not likely. Winter-run Chinook lack sufficient spatial diversity and population redundancy, making them particularly vulnerable to random events.

Despite uncertainties related to TH2, there are few remaining options for critically endangered winter-run Chinook. We recommend proceeding cautiously and using metrics such as those just proposed, with clear measures of success, to enable managers to determine if TH2 is feasible. As indicated by a population model (Lindley and Mohr 2003), however, thousands of adults and hundreds of thousands of juveniles would have to be captured and moved to recreate a viable population and much-needed spatial diversity. The most difficult question seems to be how to efficiently capture juveniles produced from natural spawning. Outmigrating juveniles need to be captured in large numbers, transported, and released in a manner that assures reasonable survival rates to adulthood. Rapid elevation fluctuations of Shasta Reservoir and high-magnitude peak flows on the McCloud River complicate capture efficiency and likely will require major investment in infrastructure with uncertain technology. The program, however, should not be independent of other potential conservation strategies. For example, reestablishing a population of winter-run Chinook in Battle Creek, a spring-fed tributary to the Sacramento River, should have a high priority, despite difficulties in dealing with dams and complex hydroelectric infrastructure.

Although spring-run Chinook have been denied access to most of their historical spawning habitat (NMFS 2014), the case for using TH2 as an emergency measure is less compelling than for winter-run Chinook. Three independent wild spring-run Chinook populations continue to persist in the Sacramento drainage (Deer, Mill, and Butte Creeks), although these neighboring populations are vulnerable to extirpation (Moyle et al. 2017; Thompson et al. 2012). There is also a population in the Feather River, which is hybridized with fall-run fish and influenced by hatchery production. Recent evidence also suggests that spring-run Chinook viability and spatial diversity may be improving with the recent recolonization of Battle and Clear Creeks and the apparent return of phenotypic spring-run Chinook to several San Joaquin River tributaries (NMFS 2016). Strong consideration has to be given as to whether the considerable resources involved in a TH2 effort could be better used to support other actions to benefit the salmon. Examples include improving access to floodplain rearing habitat for juveniles, improving spawning habitat in the lower Yuba River, and providing volitional passage for adult salmon over Englebright Dam on the Yuba River.

CONCLUSIONS

TH is a common strategy to get Pacific Coast salmonids over dams, involving millions of fish each year (Anderson et al. 2014). However, there is no TH2 program that can be declared an unequivocal success. The most successful programs, such as on the Baker River, have evolved over decades and are not solely reliant on TH2 but also supplement with hatchery fish, which may provide most of the adult returns. Capturing large numbers of outmigrating juveniles is the greatest management hurdle for TH2 programs, although all aspects of such technology-dependent conservation programs face challenges. Still, in places like California's Central Valley, few options remain to increase numbers of threatened and endangered salmonids and time is quickly running out (Katz et al. 2013). TH2 may be most appropriate for critically endangered fish where few remaining options exist, but even in these cases such a program should (1) clearly define measurable and objective success metrics, (2) proceed experimentally under an adaptive management framework to determine risk–benefit trade-offs, and (3) move in parallel with long-term comprehensive conservation strategies that consider the entire life cycle of the species.

The reality is that a TH2 program will not save winter- or spring-run Chinook in California but only prolong their decline to extinction unless significant policies addressing limiting factors on the entire life cycle of the species are put into place. Such strategies include dam removal (Quiñones et al. 2015), restoration of historical floodplain habitat throughout the Central Valley (Sommer et al. 2001), upgrading water infrastructure (Hanak et al. 2011), managing timing and magnitude of reservoir release flows to mimic natural hydrographs (Kiernan et al. 2012), and improving juvenile out-migration routes through the San Francisco Estuary. Structured decision analysis tools (Gregory et al. 2012a; Gregory et al., 2012b) may also be particularly useful in determining trade-offs between different conservation strategies while providing insight into the best combination of strategies to improve population abundance and resilience. The key question for any TH2 program must focus on how well it contributes to returning adult fish and to maintaining or increasing the total population.

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