

Conservation of Native Fishes of the San Francisco Estuary: Considerations for Artificial Propagation of Chinook Salmon, Delta Smelt, and Green Sturgeon

Joshua A. Israel¹, Kathleen M. Fisch², Thomas F. Turner³, and Robin S. Waples⁴

ABSTRACT

Many native fishes in the San Francisco Estuary and its watersheds have reached all-time low abundances. Some of these declining species (e.g., Chinook salmon *Oncorhynchus tshawytscha*) have been under artificial propagation for decades. For others (e.g., delta smelt, *Hypomesus transpacificus*, and green sturgeon, *Acipenser medirostris*), this management option is just beginning to be discussed and implemented. Propagation strategies, in which organisms spend some portion of their lives in captivity, pose well-documented genetic and ecological threats to natural populations. Negative impacts of propagation have been documented for all Central Valley Chinook salmon runs, but limited efforts have been made to adapt hatchery operations to minimize the genetic and ecological threats caused by propagated fishes. A delta smelt propagation program is undergoing intensive design and review for operations and monitoring. However, if limiting factors facing this species in its estuarine habitat are not effectively addressed, captive propagation may not be a useful conservation approach, regardless of how carefully the propagation activity is designed or monitored. Scientifically

defensible, ecologically based restoration programs that include monitoring and research aimed at quantifying natural population vital rates should be fully implemented before there is any attempt to supplement natural populations of delta smelt. Green sturgeon are also likely to face risks from artificial propagation if a large-scale program is implemented before this species' limiting factors are better understood. In each of these cases, restoring habitats, and reducing loss from human actions, are likely to be the best strategy for rebuilding and supporting self-sustaining populations.

KEY WORDS

risk assessment, genetic management, effective population size, diversity, ecosystem management

INTRODUCTION

Humans have invested substantial time and money into regulating rivers in California and the western United States to provide predictable and reliable water supplies for agriculture, urban use, and flood protection (Hughes and others 2005; Lund and others 2007). Construction of dams and large water diversions, extensive invasion by non-native organisms, and water pollution have combined to imperil many fish species and populations endemic to California's Central Valley (Yoshiyama and others 1998; Matern

¹ Dept. of Animal Science, University of California, Davis.
Current address: Applied Science Branch, U.S. Bureau of Reclamation;
jaisrael@usbr.gov

² Dept. of Animal Science, University of California, Davis.

³ Museum of Southwestern Biology, University of New Mexico, Albuquerque.

⁴ Northwest Fisheries Science Center, NOAA-Fisheries Service.

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

and others 2002; Brown and Moyle 2005; Sommer and others 2007). Increasingly, fishery agencies are propagating native fishes and raising them in captivity to supplement natural populations and reintroduce species to habitats from which they have disappeared (Utter and Epifanio 2002; Flagg and others 2004; Lichatowich 1999). Artificial propagation is the breeding and rearing of individuals within a captive environment that are subsequently released to the wild. In California, propagation of native fishes occurs for three major purposes:

1. legal mitigation for lost habitat,
2. fishery enhancement to increase the number of fish available for harvest, and
3. conservation efforts to reduce short-term risks to natural populations while limiting factors of decline are addressed.

Over the past century, efforts for salmonid propagation in California have focused on the first two purposes.

Although artificial propagation can provide abundant fish for restocking, this strategy cannot replace the abundance, productivity, life history diversity, and broad distribution characteristic of viable populations. In many hatchery programs, operational practices are not formulated to minimize risks to natural populations, but instead focus on successfully producing high juvenile survival and positive adult replacement rates (Waples and others 2007). Reducing uncertainty about the benefits and risks of propagation for mitigation and enhancement has led to increased research on this topic, with a majority observing genetic and ecological risks associated with supplementing the natural population with hatchery fishes (Cross and King 1983; Washington and Koziol 1993; Hilborn 1992; Levin and others 2001; Levin and Williams 2002; Minckley and others 2003; Araki and others 2008). Conservation-oriented mitigation and enhancement propagation programs have been reviewed extensively, and many recommendations have been made for further evaluation, research, and monitoring to minimize genetic and ecological risks to natural fish populations (Waples and Drake 2004; Mobrand and others 2005; Fraser 2008; McClure and

others 2008; Naish and others 2008; George and others 2009; Kostow 2009). Recommendations included in more than one of these articles suggest that to maximize potential benefits, and to help minimize risks, the following strategies should be considered:

- Implement only propagation programs that benefit natural populations.
- Create scientifically defensible hatchery programs that can adapt to new information.
- Scale hatchery programs to fit the natural carrying capacity.
- Use acclimation ponds and volitional releases for juveniles that will promptly out-migrate.
- Locate large releases of hatchery fishes away from important natural production areas.
- Restrict the number of hatchery adults allowed into natural production areas.
- Mark 100% of the hatchery fish to monitor the effects of hatchery programs.

More recently, artificial propagation has emerged as a component of recovery programs for species listed under the federal Endangered Species Act (ESA). These experimental propagation programs are distinct from enhancement and mitigation propagation programs; experimental programs typically include intensive research and monitoring of their genetic and ecological impacts on natural conspecifics because their goals are, principally, for experimental reintroductions, translocations, or refugial/sanctuary purposes (Minckley 1995; Stockwell and Leberg 2002; Goldsworthy and Bettoli 2006; Osborne and others 2006). Often, a primary goal of ecosystem restoration programs is to increase natural productivity and abundance of fish populations so they can remain viable in a restored, functioning ecosystem. Artificial propagation can be critical in active reintroductions to provide enough fish to re-establish genetically diverse populations. Propagation also can be useful for producing fish for experiments to increase managers' understanding of the biological and technological feasibility of these activities. Restoration activities that involve reintroduction of artificially propagated salmonids are planned for the San Joaquin

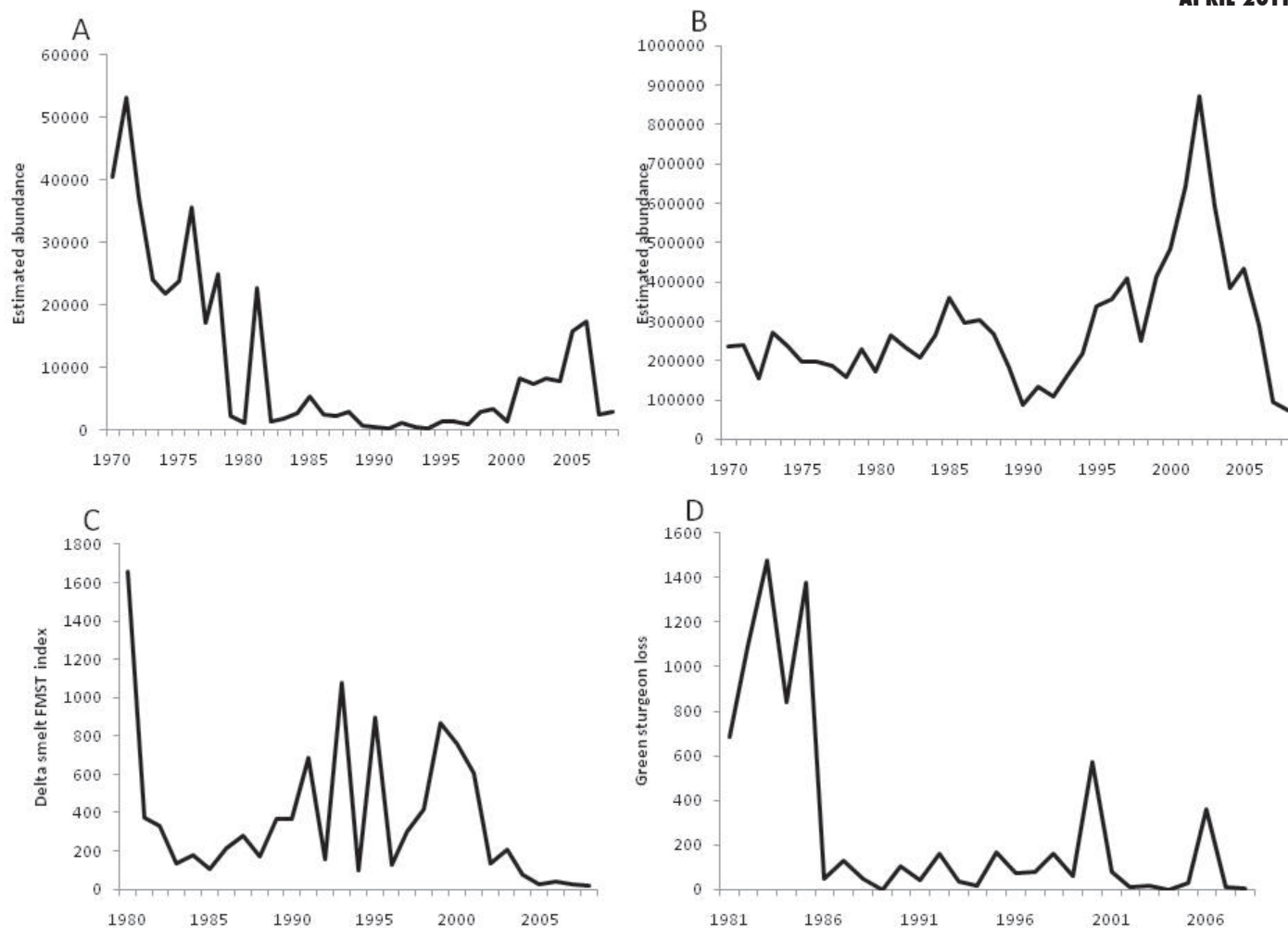


Figure 1 Trend in abundance for winter-run Chinook (A) and fall-run Chinook (B) from the CDFG Grandtab data table. Green sturgeon loss at the SWP and CVP (C) and the Fall Midwater Trawl index of delta smelt (D) are presumed to reflect trends for these species in the Bay-Delta. Fall Midwater Trawl index of delta smelt (C) and green sturgeon salvage at the SWP and CVP (D) are presumed to reflect trends for these species in the Bay-Delta.

River basin (SJRRP 2010) and the Sacramento River basin (NMFS 2009). Also, the Bay Delta Conservation Plan (BDCP) for the San Francisco Estuary is proposing conservation measures that reduce the genetic and ecological impacts of hatcheries on salmonid populations as well as establish genetic refugia for delta smelt (*Hypomesus transpacificus*) and longfin smelt (*Spirinchus thaleichthys*) (BDCP 2009).

This paper was developed in consideration of two recent workshops in California's Central Valley. The first, held in 2008, was titled "The use of artificial propagation as a tool for Central Valley salmonid and delta smelt conservation"¹, and the second, held

in 2010, was titled "Imperiled Bay-Delta aquatic species: How an aquatic technology center can help address conservation needs"². Both explored the benefits and risks of artificial propagation as part of recovery strategies for imperiled fishes in the San Francisco Estuary and watershed. Given continued reliance on propagation programs for native California fishes, there is value in scrutinizing management efforts to integrate propagation into current and future fish restoration efforts. Here, we develop case studies on artificial propagation for three species: Chinook salmon (*Oncorhynchus tshawytscha*), delta smelt, and green sturgeon

² <http://caba.ucdavis.edu/seminars/march-15-2010>

¹ http://www.science.calwater.ca.gov/events/workshops/workshop_ap.html

Table 1 Life history and ecological characteristics of Central Valley species where artificial propagation is ongoing or being considered

Characteristic	Chinook salmon	Delta smelt	Longfin smelt	Green sturgeon
Mating system	semelparous, female mate choice, nest	semelparous, group broadcast	semelparous, suspected group broadcast	iteroparous, group broadcast
Incubation strategy		Planktonic		
Fecundity	2,000 – 17,000	1,000 – 2,600	5,000 – 24,000	60,000 – 140,000
Generation length	3 years	1 year	2 years	unknown
Longevity	5 years			40 years
Age at first maturity	2 years	1 year	2 years	15 years
Number of year classes spawning together	1 to 4, typically 2	1	1	Unknown, but suspected to include many classes
Maximum size (mm)	1,500	50 – 70	120	2,300
Sampled in habitat surveys	Yes	Yes	Yes	Yes
Exploitation (Harvest) rates monitored	Yes	No	No	No
Monitored at location of limiting factors	Yes	Yes	Yes	Yes
Genetic markers	Yes	Yes	Yes	Yes

(*Acipenser medirostris*). These fish have very diverse life histories and have been the subjects of distinct management strategies both in captivity and in the wild (Table 1). We consider previously published reviews and recommendations about propagation of these species, in light of their biology, to consider whether propagation can be effectively used to conserve the species. Since it is likely additional aquatic species recovery and restoration programs in California will consider propagation (Table 2), we develop a list of critical issues to address in propaga-

Table 2 Fish species native to the California Central Valley that were recently discussed by presenters in two workshops as potentially in need of artificial propagation and establishment of refugial populations if their current status continues to decline

Sacramento perch	<i>Archoplites interruptus</i>
Hitch	<i>Lavinia exilicauda</i>
Sacramento blackfish	<i>Orthodon microlepidotus</i>
Sacramento splittail	<i>Pogonichthys macrolepidotus</i>
Longfin smelt	<i>Spirinchus thaleichthys</i>
White sturgeon	<i>Acipenser transmontanus</i>
Green sturgeon	<i>Acipenser medirostris</i>

tion planning and implementation and provide ideas about how to reduce these uncertainties.

ARTIFICIAL PROPAGATION OF CENTRAL VALLEY CHINOOK SALMON

Chinook salmon are an iconic anadromous fish native to the coastal river systems draining into the northern Pacific Ocean (Healey 1991). Their general life history in the Central Valley is well-known, and the interested reader is referred to other publications for additional details of their biology and status (Williams 2006; Moyle and others 2008). Four distinctive populations of Chinook salmon (fall-run, late fall-run, winter-run, and spring-run) compose three Evolutionarily Significant Units (ESUs) in the Central Valley. The ESUs are named for the seasonal timing of their reproductive migrations from the Pacific Ocean to their natal streams. We focus on fall-run and winter-run Chinook salmon because they both have propagation programs with distinct purposes. Fall-run Chinook salmon have been propagated for mitigation and enhancement purposes due to lost habitat, while winter-run Chinook salmon have been under limited and carefully managed conservation propagation for two decades because of their low abundance.

Fall-run Chinook salmon occur throughout the Central Valley, but their distribution has been greatly reduced in all major Central Valley streams (Yoshiyama and others 1998). Winter-run Chinook salmon spawning is restricted to a single reach of the Sacramento River below Keswick dam (Lindley and others 2006). Prior to Shasta and Keswick dams, winter-run Chinook ascended into the upper Sacramento River watershed to spawn and incubate their eggs in higher elevation spring-fed rivers draining Mount Shasta and the southern Cascade Range. The winter-run Chinook salmon is the most evolutionarily divergent of Central Valley salmon ESUs, and its migration timing is unique among Chinook salmon throughout the range of this complex species (Williams 2006).

Mitigation and Enhancement Propagation for Fall-Run Chinook

Fall-run Chinook salmon hatcheries were initiated as surrogates for lost habitat and the concomitant loss of salmon productivity resulting from dams. While hatcheries have successfully produced numerous fish for commercial fisheries, they have not contributed to preventing the initial or continued degradation of freshwater spawning, incubating, and rearing habitats (Lichatowich 1999). Considerable effort has been made to evaluate hatchery risks to minimize impacts on the natural population of Chinook salmon, although changes have not kept up with these reviews. The California Department of Fish and Game (CDFG) and the National Marine Fisheries Service (NMFS) Joint Hatchery Review (CDFG and NMFS 2001), as well as an Environmental Impact Statement (Jones and Stokes 2009) for the California state hatchery system, identified numerous propagation risks. These reviews identified ecological effects such as predation and competition, high harvest-exploitation rates, and loss of diversity from genetic interbreeding, which impacted natural populations of Chinook salmon.

Central Valley fall-run Chinook hatcheries are terminal, which means they were built at the base of dams. The location of these hatcheries is problematic, since extremely limited spawning habitat is available to separate natural and hatchery fishes on the spawn-

ing grounds. Restricting hatchery fish from spawning grounds used by natural-origin fish promotes spawning between natural-origin fishes, which reinforces local adaptation in the population (Chilcote 2003; Goodman 2005; Kostow 2009). Efforts to actively separate hatchery spawners from natural spawners on natural spawning grounds and in the hatchery broodstock may reduce the risks of genetic and behavioral selection for the hatchery environment that can be maladaptive in the wild over generations (Kostow 2004; Araki and others 2007; Pearsons and others 2007). At the Feather River Hatchery, interbreeding between fall-run and spring-run Chinook salmon has led to introgression of both stocks (Garza and others 2007), making broodstock management and natural production management even more difficult.

Current levels of genetic similarity among Central Valley fall-run Chinook stocks are atypically high for a large basin such as the Sacramento-San Joaquin (Garza and others 2007; Narum and others 2008). Potential reasons for homogeneity between Central Valley Chinook salmon is that many juvenile hatchery fish are transported from hatcheries and released into the San Francisco Bay to bypass low survival conditions in the rivers and estuary. Transport of juvenile salmonids increases straying and may be the reason that fall-run Chinook appear genetically homogenized with a single gene pool (Williamson and May 2005). Another potential reason for this lack of diversity is that some historically more distinctive populations were exterminated by dam development. Broodstock and juvenile emigration management strategies at hatcheries, which reduce genetic and life history diversity, may increase the susceptibility of Central Valley fall-run Chinook salmon to environmental mortality driven by ocean ecosystem food web productivity cycles (Lindley and others 2009).

Hatchery production of fall-run Chinook salmon (Table 3) has likely exceeded the carrying capacity of rivers and possibly even coastal ocean systems, where stocked fish cause predation and competition with natural populations. This reduces survival of hatchery and wild fish (Hawkins and Tipping 1999; Levin and others 2001; Nickelson 2003; Jonsson and Jonsson 2006; Kostow and Zhou 2006; Pearsons 2008). A recent report (Lindley and others 2009) sug-

Table 3 Current Central Valley salmonid hatchery operations. Fish are released in river proximal to the hatchery unless noted in the footnote. (Sources: Data updated from DFG 2001; BDCP 2009; Jose Setka, EBMUD, pers. comm.; Kevin Niemala, USFWS, pers. comm.)

Hatchery	Species	Production Goal	Broodstock Strategy	Release Strategy	% Marked	CWT%	Status of HGMP
Coleman NFH	Sacramento River Fall-run Chinook	12,000,000	Integrated ^a	Smolts	25% ^d	25%	Biological Assessment in HGMP format, submitted in 2001
	Sacramento River Late Fall-run Chinook	1,000,000	Integrated ^b	Smolts	100% ^d	100%	Biological Assessment in HGMP format, submitted in 2001
	Central Valley Steelhead	600,000	Segregated, marked fish used for broodstock ^b	Yearlings	100% ^d	0%	Biological Assessment in HGMP format, submitted in 2001
Livingston Stone NFH	Sacramento River Winter-run Chinook	200,000	Integrated ^b	Smolts	100% ^d	100%	Biological Assessment in HGMP format, submitted in 2001
Feather River Hatchery	Sacramento River Fall-run Chinook	8,000,000	Integrated ^a	Smolts ^c	25% ^d	25%	Draft in process
	Sacramento River Spring-run Chinook	2,000,000	Integrated ^b	Subyearling ^c	100% ^d	100%	Draft in agency review
	Central Valley Steelhead	450,000	Integrated ^b	Yearlings ^c	100% ^d	0%	Draft in process
Nimbus Hatchery	Sacramento River Fall-run Chinook	4,000,000	Integrated ^a	Smolts ^c	25% ^d	25%	Draft in process
	Central Valley steelhead	430,000	Segregated, marked fish used for broodstock ^b	Yearling ^c	100% ^d	0%	Draft in agency review
Mokelumne Fish Hatchery	Sacramento River Fall-run Chinook	5,400,000	Integrated ^a	Smolts ^c	25% ^d	25%	Draft in process
	Central Valley Steelhead	250,000	Integrated ^b	Yearlings ^c	100% ^d	0%	Revised draft in agency review
Merced Fish Hatchery	Sacramento River Fall-run Chinook	650,000	Integrated ^a	Smolts and Yearlings	100% ^d	100%	No development

a. At unmeasurable rate with natural populations.

b. At measurable rate with natural populations.

c. Trucked from hatchery to lower rivers and Delta.

d. Adipose clip.

gests that reduced productivity and carrying capacity in freshwater, estuary, and ocean environments played a role in the collapse of the Sacramento River fall-run Chinook stock. Pearsons (2010) presented the adaptive stocking concept that provides a decision-making framework, based on ecological indices, to balance the benefits and risks of hatchery production and stocking.

Conservation Propagation for Winter-Run Chinook Salmon

As a result of the precipitous decline in winter-run Chinook salmon escapement, and the restrictive availability of cold water habitat below Keswick Dam, a conservation propagation program was initiated for winter-run Chinook salmon in 1989 at Coleman

National Fish Hatchery (NFH) on Battle Creek, a tributary close to Keswick on the Sacramento River. An intensive effort was initiated in 1991 and continued until 2003 to raise a portion of the hatchery offspring captively to adulthood at UC Davis's Bodega Marine Laboratory and the California Academy of Science's Steinhart Aquarium as a genetic refugium. From 1999 to 2007, broodstock were captively raised at Livingstone Stone NFH, although this program was phased out as natural spawners became abundant enough to reduce risks associated with low spawner abundance in the Sacramento River to acceptable levels. Efforts with captive rearing functioned primarily as a backup to the hatchery population released into the environment, in case the natural population completely collapsed due to spawning and rearing habitat loss associated with high water temperatures from Shasta Dam.

Physical marking of all propagated winter-run Chinook salmon, and intensive genetic monitoring involving the captive and natural winter-run populations, has provided critical insight for the planning, implementation, and evolution of the winter-run Chinook propagation program. Captive populations can pose serious risks when allowed to reproduce with a small natural population because the offspring representative of captive adults can swamp that of the natural population's effective population size (N_e) and thereby affect future fitness of the wild population (Ryman and others 1995). Thus, early in the winter-run Chinook propagation program, the effective population size (N_e), a measurement of the idealized population size in which all parents have an equal expectation of being the parents of any individual, was evaluated annually to manage the hatchery program's influence on the natural population (Hedrick and others 1995). In 1992, a breeding protocol was instituted which sought to maximize the N_e from the captive spawners by equalizing their contributions to subsequently released progeny (Hedrick and others 2000a). These initial efforts to focus intensive monitoring on characterizing the effective and census population sizes of the hatchery and natural population were instrumental in successfully minimizing risks associated with broodstock management in the winter-run Chinook salmon propagation program.

Documentation of the impact of hatchery fish on naturally spawning winter-run population has also required significant field efforts to undertake spawner and carcass surveys. These surveys relied upon physical marking and coded wire tagging of hatchery fish to identified spawners as hatchery or natural origin. Between 2001 to 2009, 6% to 20% of the returning spawners of the total run were of hatchery origin (USFWS 2009). Although hatchery-origin spawners were not identified to captive parents as in Hedrick and others (2000b), there appeared to be widespread returns across coded wire tag groups over this period, suggesting that the genetic contributions to natural spawning were being spread fairly broadly among many different captive parents.

ARTIFICIAL PROPAGATION OF DELTA SMELT

Delta smelt are an annual pelagic fish endemic to the fresh and brackish waters of the San Francisco estuary. Their biology has been reviewed extensively in response to a significant decline in abundance, which prompted their listing as threatened under the ESA in 1993 (USFWS 1993; Bennett 2005). Despite ESA listing, delta smelt have continued to decline because of the intersection of its habitat with the hydraulic influence of the large federal and state water diversions and other ecological changes (Moyle and others 1992; Bennett 2005; Feyrer and others 2007; Thompson and others 2010). High summer water temperatures, reduced water quality from urban and agricultural runoff, and competition with and predation by introduced species also may contribute to the delta smelt decline.

Estimates of delta smelt adult population sizes have low precision, but decline in abundance indices are well documented (Bennett 2005; Newman 2008). Abundance estimates can vary by an order of magnitude between successive months, and sometimes exhibit confidence intervals of the same order of magnitude as the estimates. During the 1990s, the population rebounded to an estimated population size in the low millions following estimates in the early 1990s of a population size in the tens of thousands of individuals (Newman 2008). Since 2003, the frequency of monthly population estimates of fewer

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

than 100,000 individuals has increased and the population has not rebounded.

In 2008 and 2009, California Senate Bills 994 and 207 proposed a delta smelt propagation program to mitigate for those fish directly entrained in the state and federal water diversions, as well as for other anthropogenic stressors such as water pollution that result in 'take' of delta smelt. The goals of this type of mitigation program would purportedly increase delta smelt abundances to allow continued water exports and activities in the Sacramento–San Joaquin Delta through state and federal water projects that jeopardize delta smelt. These legislative bills did not pass and currently a mitigation hatchery is not planned for delta smelt. A delta smelt conservation propagation program exists as a genetic refugium for the species to safeguard its existence in the face of its extinction in the San Francisco Estuary.

Conservation Propagation for Delta Smelt

The delta smelt conservation propagation program was initiated in 2007, and is currently housed in two locations. The primary population is held at the UC Davis Fish Conservation and Culture Laboratory (FCCL), which has produced delta smelt for scientific research for over a decade. In 2007, the facility shifted to serving as a conservation hatchery to house a genetic refugium for the species. The replicate broodstock population is maintained at Livingston Stone NFH to avoid risks associated with catastrophic loss at either facility.

The FCCL delta smelt conservation propagation plan focuses on minimizing genetic risks. It operates with an intensive culture plan (Baskerville–Bridges 2005) and standard operating procedure for managing genetic diversity. Every parent in each generation is genetically characterized to minimize inbreeding and mean kinship, and pedigree analysis is performed to equalize family representation within the broodstock. The captive population is genetically monitored every generation to evaluate how well the conservation propagation plan maintains genetic diversity and N_e . These strategies were evaluated prior to spawning

the F1 generation fish, and one study concluded that the program effectively retained the genetic diversity of the founding wild broodstock (Fisch and others 2009).

The delta smelt genetic management plan is designed to:

1. retain genetic diversity of delta smelt,
2. produce fish that are genetically and ecologically similar to wild fish, and
3. maximize the effective population size.

Continued intensive genetic management of the delta smelt conservation propagation program will theoretically produce both delta smelt that are genetically and ecologically similar to wild delta smelt and serve as a refugium for the species. Wild individuals are incorporated into each generation to minimize genetic drift and maintain genetic diversity in the captive population. However, the ability for captively propagated delta smelt to survive in the natural environment is highly uncertain and intensive field research will be necessary to determine if propagated fish are ecologically similar to natural delta smelt.

Mitigation Propagation for Delta Smelt

A mitigation hatchery for delta smelt will need to maintain a genetic bank in a captive population suitable for reintroduction into the Bay–Delta, while still producing very large numbers of fish needed to mitigate water diversion impacts and to supplement depleted wild populations. Additionally, efforts to supplement the natural population may require collecting adults from the Bay–Delta that are genetically and phenotypically representative of the natural population and not progeny of the refugial hatchery program, so as to produce ecologically diverse hatchery fish. A broodstock collection effort of this size seems extremely difficult, given the low abundance of adult delta smelt and the physical health of most captured fish.

An essential consideration for such a propagation effort is intensive monitoring of the natural population's abundance and spawning distribution. This information is necessary to inform what level of

production will not swamp the natural population's genetic diversity. An integrated hatchery might include both enhancement and genetic viability as primary goals. Research on captive Rio Grande silvery minnow (*Hybognathus amarus*) suggests that it is difficult to balance these goals (Osborne and others 2006), but more recent data have indicated that benchmarks for production and genetic diversity can be simultaneously met when there is careful coordination among propagation, enhancement, and genetic monitoring efforts (Turner and Osborne, unpublished). However, meeting these objectives is increasingly difficult, as the wild population continues to decline and as collection of broodstock is further curtailed to ensure maximum protection of the wild population.

If a propagation program were to be designed to supplement the wild population, the low precision of estimates of natural population census size would make it difficult to determine what number of delta smelt would minimize risks associated with reintroduction. At the necessary scale of production, it would be very difficult for a conservation hatchery to: (1) produce delta smelt with full regard for the proportion of non-hatchery origin broodstock introduced relative to the wild population or (2) genetically monitor hatchery families. To maintain adequate numbers of broodstock, the conservation hatchery might even maintain delta smelt in captivity across multiple generations without supplementing the broodstock with wild fish each year. These practices could contribute to decreased genetic diversity and increased inbreeding in the captive population, as well as integration of broodstock across captive generations.

A mitigation hatchery for delta smelt should be expected to create all the same risks for the natural population as a salmonid hatchery (i.e.: loss of genetic diversity, domestication selection, impairment of carrying capacity available to the natural population). A hatchery intended to adequately mitigate for entrainment loss should reintroduce more than 100,000 juvenile delta smelt per year into the Bay-Delta system, to match the peak numbers salvaged at the federal and California fish facilities (Table 4). For instance, based on its water diversion restrictions, the current delta smelt biological opinion

Table 4 Numbers of young-of-year delta smelt counted in fish salvage operations of the Banks and Jones Pumping Plants, estimates of percentages of the population entrained taken from Kimmerer (2008) and estimates of subsequent sizes of the maturing adult population based on the CDFG's Fall Midwater Trawl Survey (September–December averages from Newman 2008).

Year	Age-0 Salvage ^a	Percent of Adults Entrained	Percent of Age-0 Entrained	Average Fall Abundance (Millions of Fish)
1995	24		~0.0	1.8
1996	39,823		1.7	0.24
1997	42,091		14.0	0.56
1998	242		~0.0	0.74
1999	153,041		7.7	1.7
2000	101,790		14.0	1.7
2001	15,984		19.0	1.2
2002	59,683	15	26.0	0.24
2003	26,261	50	17.0	0.36
2004	12,441	19	20.0	0.09
2005	1,734	7	3.1	0.042

^a Recently estimated to be <10% of the number entrained at the State Water Project intake to Clifton Court Forebay.

expects entrainment to remain in the low thousands of individuals (USFWS 2008a). Thus, even without population recovery as a goal, at current low population levels, a mitigation hatchery should expect to produce thousands of fish annually to mitigate for water diversions at levels preceding the recent court-ordered and ESA-mandated reductions (Table 4).

ARTIFICIAL PROPAGATION OF GREEN STURGEON

Green sturgeon are long lived, iteroparous, anadromous fish with known spawning populations in the Sacramento, Klamath, and Rogue rivers (Adams and others 2007). Fishing is prohibited for green sturgeon in California, except for in-river tribal fisheries on the Klamath and Trinity rivers. The Sacramento River contains the only spawning populations in the southern Distinct Population Segment (DPS), which was listed as threatened under the ESA in 2006 (Adams

and others 2007). Its biology was reviewed by Israel and Klimley (2009). The abundance of the population is unknown. Adults are rarely observed in the Sacramento River and fewer juveniles are observed in the river and estuary than for the more common white sturgeon (*A. transmontanus*). Spawning habitat is limited to a small segment of the Sacramento River and habitat utilization by early life history stages is not well described (Heublein and others 2008; Poytress and others 2009).

Recruitment from the Sacramento River is cyclic, and presumably, adults in the ocean serve as a reservoir of spawners when abiotic and biotic processes overlap to promote favorable survival of larvae and juveniles. Recruitment failures due to low survival of the earliest life history stages is a significant bottleneck for other North American acipenserids, such as pallid sturgeon (*Scaphirhynchus albus*) and the white sturgeon in the Upper Columbia and Kootenai rivers. The populations of the latter have numerous reproductive adults, but few recently surviving wild juveniles (Duke and others 1999; Hildebrand and others 1999; Korman and Walters 2001). A recovery plan for green sturgeon in the Sacramento River has not been developed, although viability analyses suggest the population is most sensitive to changes in survival of adults (Beamesderfer and others 2007; Heppell 2007). Artificial propagation could be considered to meet this objective by increasing the abundance of adults, but given the long life span of these fish, it is unlikely to influence the number of spawners in the river for decades.

Conservation Propagation for Green Sturgeon

A conservation hatchery for green sturgeon would likely be similar to other conservation artificial propagation being pursued in North American sturgeon recovery plans. These recovery programs have developed conservation hatchery programs (Paragamian and others 2005; USFWS 2005) to increase survival associated with ecological factors potentially limiting green sturgeon survival during the earliest freshwater stages of their life cycle. Atlantic and pallid sturgeon captive-rearing and broodstock programs have been established when populations are suspected to have

reached critical levels of endangerment (Henderson and others 2005; USFWS 2005). In hatchery programs for Kootenai white sturgeon and pallid sturgeon, there are concerns that each species will go extinct in the wild before hatchery adults are mature enough to integrate into the natural spawning population, although this risk has not been established for green sturgeon. Where there is difficulty in obtaining sturgeon in the wild and a need for fish for experimental purposes exists, artificial propagation has been advanced (Van Eenennaam and others 2008). Regardless, given the uncertainty about the abundance and population dynamics of green sturgeon and its viability, it is unknown whether a conservation hatchery is necessary for the species.

Enhancement Propagation for Green Sturgeon

Clear objectives are necessary for any propagation approach. The census population of southern DPS green sturgeon is presumably viable, since the species is long-lived and migratory, fishing is restricted, and annual adult survival is estimated to be high (Lindley and others 2008). However, the annual breeding population has been estimated to be quite small (Israel and May 2010). With high fecundity from a single female, a large-scale operation may erode the species' genetic diversity in only a few captive-bred generations. Offspring from a small number of broodstock may swamp naturally produced fish. Green sturgeon spawning periodicity is between 2 and 4 years based on telemetric data (Erickson and Webb 2007), and the reproductive success of an individual in multiple years is likely not equivalent since interannual abiotic factors such as water temperature and flow likely influence the mortality of early life history stages. Green sturgeon recruitment appears highly variable (CDFG, unpublished data), suggesting that annual supplementation from a hatchery might not mimic the current population demography.

Fisheries enhancement hatcheries for sturgeon exist in the Caspian and Azov seas, where multiple countries actively pursue artificial propagation to support caviar fisheries. These countries often release many millions of fingerlings (1 to 2 months of age, 3 to 5 grams), and scientists have identified insufficient

sampling to assess return rate and interactions of the hatchery–origin sturgeons, genetic information on current broodstock, and information about economic benefits of propagation at this scale (Abdolhay and Tahori 2006). In the Sea of Azov, broodstock management practices at fisheries supplementation facilities led to truncation of the spawning timing and reproductive season of sturgeon, as well as shifts in genetic composition (Chebanov and others 2002). Since few females are necessary to produce large numbers of juveniles, domestication and reduction of effective population size are the significant risks of this approach for green sturgeon.

Scientists recognizing the negative impact of sturgeon broodstock management in the Caspian and Azov seas called for additional ecological studies to develop new approaches for sturgeon stocking, as determined by their life history. These approaches included seasonality of reproduction age and size of released juveniles, and the influence of climatic variation on the productivity of brackish lagoons and coastal areas (Chebanov and others 2002). Release strategy and ecological interactions have been related to density- and size-dependent mortality of propagated Kootenai white sturgeon juveniles (Justice and others 2009). Due to the longevity of green sturgeon, hatchery and natural populations would be difficult to integrate, and the objective for a segregated hatchery would have to be determined.

A NEW HATCHERY DYNAMIC FOR THE CENTRAL VALLEY

Operational procedures for a majority of propagation activities in the Central Valley have focused on population supplementation because that was their long-standing mandate. Published evaluations and regional reviews of supplementation programs suggest that changes are necessary if managers desire to meet emerging conservation-based goals such as reducing the genetic and ecological risks inherent in artificial propagation. If propagation efforts move forward to increase the number of species being brought into captivity for some stage of their life cycle, each effort requires a framework to evaluate its own protocols in light of the distinct genetic, ecological, and demographic make-up of the species. HGMPs provide

detailed information about operation of propagation activities; although, to adequately address risks and implement propagation in an adaptive management framework, intensive evaluations of carrying capacity and monitoring of hatchery populations in the wild are necessary (Pearsons 2010). Without an ecosystem-based perception of the status of natural populations and adequate management strategy to identify fish from both natural and hatchery populations, it is not possible to evaluate whether natural populations are responding to habitat restoration or whether hatchery fish are just replacing natural fish.

In the future, artificial propagation will likely be further emphasized in conservation of imperiled fish species, although managers have not always shown an interest in addressing the new risks associated with these activities or the underlying causes of endangerment. Thus, we recommend a distinct approach to dynamically managing populations under propagation that are imperiled by environmental and anthropocentric threats. This adaptive approach should attempt to integrate some of these considerations.

Goals and Objectives of Propagation

An important initial step toward reducing risks associated with hatcheries in California is to develop scientifically defensible objectives for propagation programs based on natural and hatchery population management goals. If the natural population management goal is recovery only, then hatchery programs must be focused on conservation. If the natural population management goal is economic, then hatchery programs should supplement wild populations without causing demographic and genetic changes that hinder their recovery and resilience.

Since propagation programs include inherent genetic, demographic, and ecological risks to natural populations, any hatchery operation must either be undertaken with best management practices that minimize domestication and maximize natural selection effects on hatchery fish, and/or it must be undertaken in concert with actions to minimize interbreeding between hatchery and natural fish. In the case of fall-run Chinook salmon, if trucking juveniles past

the Delta continues, better outplanting and brood-stock management strategies are necessary throughout the Central Valley to minimize the genetic effects of increased straying. On tributaries with both natural fall-run Chinook salmon spawning areas and hatcheries supplementing these fish, studies should evaluate the efficacy of minimizing the proportion of hatchery origin fishes spawning on the natural spawning grounds (RIST 2009). Study methods (i.e., marking and tagging) to differentiate hatchery and natural populations in the river, estuary, and ocean are essential for monitoring these different populations. It is also necessary to quantify the relationships between these different populations in different environments, and studies employing such methods can support scientifically defensible policies for propagation.

As conservation hatcheries shift from supporting refugial populations to focusing on restoring natural populations, identifying all releases will be an essential monitoring and management tool (RIST 2009). In fact, the winter-run Chinook salmon hatchery programs has gained information about the benefit of the program from the complete marking and tagging of hatchery progeny. In the case of green sturgeon and delta smelt, physical marking may not always work, and genetic tagging (see "Using Genetic Information for Broodstock Management") or other physical tags may be preferable. While scute marking, a common visual marking method of sturgeon, is unreliable because scutes grow back (J. Cech, UCD, pers. comm.), Passive Integrative Transponder (PIT) tags may prove useful since sturgeon are fairly large.

Regional Review of Propagation Programs

A key element of propagation programs is iterative, independent review (Hilborn 1992; George 2009). A statewide review of California's anadromous salmonid hatchery system, structured on the successful model of the Hatchery Reform Project, was funded in 2009 and will be initiated in 2010. This type of review will evaluate hatchery propagation from an ecosystem-based approach, and consider its impacts and its effects on carrying capacity, diversion losses, and harvest exploitation in an integrated fashion. Such reviews will stimulate recommendations that will develop into risk-averse HGMPs, as well as into

landscape-level monitoring and evaluation strategies to further adapt salmonid management. Such regional reviews should be an element of agency planning and implementation of propagation programs for any of the Bay-Delta native fishes. The development of a regional oversight committee and independent peer review of management documents are essential for advancing regional management strategies involving conservation propagation for native fish (George and others 2009).

Propagation is Just One Part of Population Rebuilding

Implementation of propagation programs, regardless of their objective, should be advanced in an ecosystem framework. Propagation activity cannot rebuild natural populations if habitats remain degraded. Often propagation is undertaken to meet multiple goals and these must all be synthesized into an integrated framework. In watersheds that could serve as natural refugia, the importance of providing suitable spawning habitat for natural fish and not swamping that habitat with hatchery fish should be considered. Population-level examination of hatchery operation and how carrying capacity, habitat availability, harvest management, and losses to diversions interact are necessary to manage and implement habitat and harvest-based measures to protect natural fish productivity and biocomplexity. Future efforts to develop ecological indices for the California Current and San Francisco Estuary, which are the first coastal environments Central Valley salmonids encounter, may allow contingencies to be developed that adapt hatchery production and stocking for the greatest net ecosystem and human benefit.

Monitoring of Natural Fish Populations

Too frequently, conservation propagation is initiated as a last resort, without the time necessary for the design or planning of such a strategy. Before the need for propagation arises, agencies should begin monitoring and evaluating declining species to proactively characterize the vital rates of natural populations. The planning process for propagation of any San Francisco Bay-Delta fishes would benefit

from initial development of comprehensive monitoring regimes for both natural populations and hatchery broodstock. These regimes could help managers assess whether hatchery program goals are being met, and if the program's genetic and ecological risks have minimal affect on the persistence of wild populations. Monitoring protocols are generally tailored to individual species to accommodate specific life-history stages when they are most easily sampled. Since propagation directly affects the fitness and survival of fish during specific captive life-history stages, (e.g., species in [Table 1](#)), monitoring of wild and hatchery populations during these life stages should include measurements to assess survival, changes in genetic diversity, shifts in phenotypic variation, loss of life-history diversity, and spatial distribution. Assessing the abundance and distribution of particular life stages, as well as the proportion of hatchery and natural fish, is necessary to determine how propagation affects life-history diversity, and whether propagation activities maintain life-history variation. Well-designed field monitoring programs that span relevant temporal and spatial scales, and focus on both wild and captive stocks, will provide necessary insight into the effectiveness of the hatchery program (Turner and others 2006). This information may be essential for developing an effective adaptive management plan to minimize risks and maximize benefits, as well as for ending the program when recovery goals are met.

Using Genetic Information for Broodstock Management

The use and interpretation of genetic data in hatchery broodstock management can improve monitoring the impacts of propagation on the conservation of native fishes by answering the following questions:

1. What is the genetic diversity of broodstock and how well do progeny reflect genetic diversity of brood and wild fish?
2. How often and how many wild fish are needed to refresh broodstock to reduce gene frequency change resulting from domestication selection and genetic drift?

3. What is the effective population size in the wild and what is the optimal number of individuals to be repatriated to balance founder effects against catastrophic failure and propagation effects?

These are all difficult questions to answer both in theory and practice, although genetic monitoring can provide useful management insight into the risks and benefits posed by propagation programs. Methods for using genetics to “family-print” all offspring of broodstock can be broadly applied within the Central Valley to understand gene flow of hatchery fish within the artificially propagated and natural populations using parental-based tagging theory (Letcher and King 1999; Anderson and Garza 2006). Propagation risks are greatest in species with high turnover rates and highly dynamic populations, such as delta smelt, since key parameters such as adult census size and N_e are difficult to estimate. By comparison, for species such as green sturgeon, these parameters can be evaluated for years before any decisions about propagation can be made.

Systematic genetic monitoring is necessary that rapidly and reliably characterizes genetic diversity of adult fishes in both natural populations and supplementation programs; monitoring should include measuring relatedness, inbreeding, and N_e ([Figure 2](#)). Ecological and genetic monitoring can be done in concert (e.g., tissues for genetic analysis taken during distribution and relative abundance surveys) and at management locations (e.g. harvest, habitat monitoring, fish salvage facilities) to integrate resources and expertise. Monitoring programs should be conducted on spatial and temporal scales that permit elucidation of relevant trends in benchmark values established during program planning (Schwartz and others 2007). Most important, monitoring efforts should provide insight into relevant spatial and temporal trends in factors that limit abundance and genetic diversity of wild stocks before, during, and after supplementation from hatchery stocks, as well as from habitat restoration and threat abatement measures. Once these insights are obtained, managers can put monitoring conclusions into practice, and can also provide feedback to the monitoring effort to hone their utility and efficiency.

Conservation Propagation Genetic Management

Standard Operating Procedure

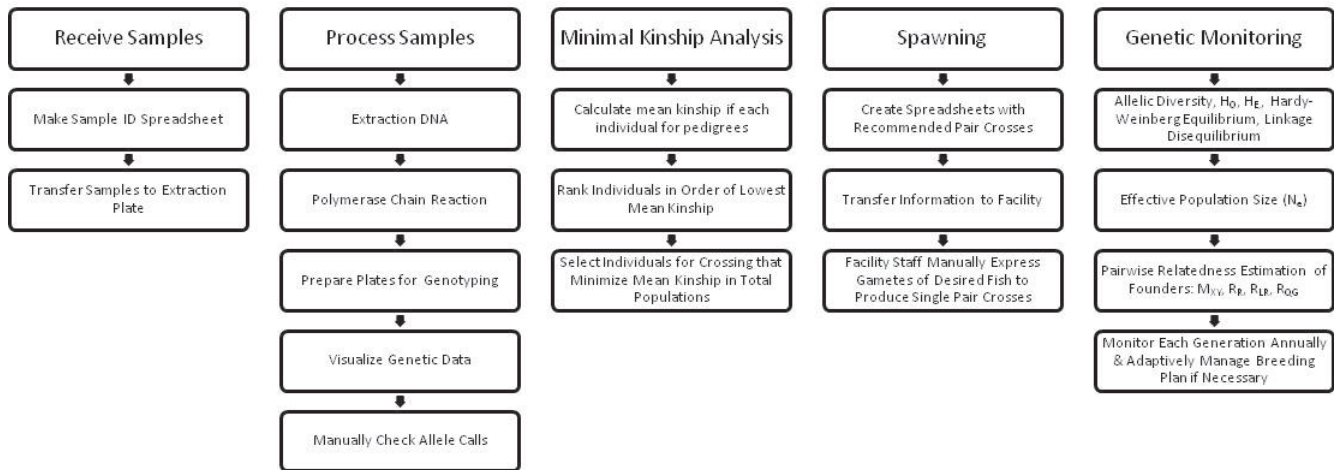


Figure 2 Genetic management procedures for conservation propagation programs (Adapted from Fisch and others, in prep.)

Biological monitoring programs are underway for declining species in the San Francisco Estuary (Table 1) and they will continue to provide important information on population trends and other aspects of the species. These monitoring programs may need to be improved to monitor both hatchery and natural populations. If propagation programs for native species are deemed necessary to meet social and/or conservation objectives, then these programs should strive to find ways to operate that do not further threaten the viability of natural populations. Managers should advance supplementation activities by operating programs based on population genetic and ecological theories, testing hypotheses about the fish under culture, and adaptively addressing emerging concerns. Conservation hatcheries that focus on maintaining the genetic diversity of imperiled species can play a critical role in preserving populations while habitats are being restored to favorable conditions. More species in California will presumably need propagation efforts to preserve them, as human demand for water increases and as the climate becomes warmer and more variable. However, management choices that view propagation as just one of the activities necessary to rebuild and recover imperiled population are likely to have the greatest success. Successful propagation efforts will work best if they focus on the environment encountered by the

fish they produce as much as on the number of fish being produced. If California’s attempts at propagation are not based on scientific principles and continued research, artificial propagation will likely further endanger the species we are attempting to conserve.

ACKNOWLEDGEMENTS

This article is a product of a workshop organized by the CALFED Science Program (http://www.science.calwater.ca.gov/events/workshops/workshop_ap.html). Former CALFED Lead Scientist Mike Healey developed the idea for the workshop. Matt Nobriga organized the workshop for the Science Program and reviewed several drafts of the manuscript. The authors appreciate useful comments on an earlier draft of this article from Lee Blankenship, Robert Clark, Cliff Dam, Bernie May, and two anonymous reviewers. The views expressed are those of the authors and do not reflect official opinions of NOAA Fisheries or the Bureau of Reclamation.

REFERENCES

Abdollah HA, Tahori HB. 2006. Fingerling production and release for stock enhancement of sturgeon in the Southern Caspian Sea: an overview. *Journal of Applied Ichthyology* 22:125–131.

- Adams PB, Grimes C, Hightower JE, Lindley ST, Moser ML, Parsley MJ. 2007. Population status of North American green sturgeon, *Acipenser medirostris*. *Environmental Biology of Fishes* 79(3–4):339–356.
- Anderson EC, Garza JC. 2006. The power of single-nucleotide polymorphisms for large-scale parentage inference. *Genetics* 172(4):2567–2582.
- Araki H, Berejikian BA, Ford MJ, Blouin MS. 2008. Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications* 1(2):342–355.
- Araki H, Cooper B, Blouin MS. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* 318(5847):100–103.
- Baskerville-Bridges B, Lindberg J, Van Eenennaam J, Doroshov S. 2005. Manual for the intensive culture of delta smelt (*Hypomesus transpacificus*). Report to CALFED Bay-Delta Program. Davis (CA): University of California, Davis p. 22.
- [BDCP] Bay-Delta Conservation Plan. 2009. Working draft conservation strategy. Sacramento (CA): California Natural Resources Agency. p. 1145.
- Beamesderfer RCP, Simpson ML, Kopp GJ. 2007. Use of life history information in a population model for Sacramento green sturgeon. *Environmental Biology of Fishes* 79(3–4):315–337.
- Bennett WA. 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. *San Francisco Estuary and Watershed Science* [Internet] Available from: <http://escholarship.org/uc/item/0725n5vk>
- Brown L, Moyle PB. 2005. Native fishes of the Sacramento-San Joaquin drainage, California: a history of decline. In: Rinne JN, Hughes RM, Calamusso B, editors. *Historical changes in large river fish assemblages of the Americas*. American Fisheries Society Symposium 45. Bethesda (MD): American Fisheries Society. p 75–98.
- Chebanov MS, Karnaukhov GI, Galich EV, Chmir YN. 2002. Hatchery stock enhancement and conservation of sturgeon, with an emphasis on the Azov Sea populations. *Journal of Applied Ichthyology* 18(4–6):463–469.
- Chilcote MW. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 60(9):1057–1067.
- Cross TF, King J. 1983. Genetic-effects of hatchery rearing in Atlantic salmon. *Aquaculture* 33(1–4):33–40.
- [CDFG and NMFS] California Department of Fish and Game, National Marine Fisheries Service. 2001. Final report on anadromous salmonid fish hatcheries in California. Sacramento (CA): California Department of Fish and Game, Fisheries Branch. 40 p.
- Duke S, Anders PJ, Ennis G, Hallock R, Hammond J, Ireland SC, Laufle J, Lauzier R, Lockhard L, Marotz B and others. 1999. Recovery plan for Kootenai River white sturgeon (*Acipenser transmontanus*). *Journal of Applied Ichthyology* (15):157–163.
- Erickson DL, Webb MAH. 2007. Spawning periodicity, spawning migration, and size at maturity of green sturgeon, *Acipenser medirostris*, in the Rogue River, Oregon. *Environmental Biology of Fishes* 79(3–4):255–268.
- Feyrer F, Nobriga ML, Sommer TR. 2007. Multidecadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 64:723–734.
- Fisch K, Rettinghouse T, Ellison L, Tigan G, Lindberg J, May, B. 2009. Delta smelt refugial population development and genetic management—2009 season summary. *Interagency Ecological Program Newsletter* [Internet]. Summer/Fall 2009. 22(3):3. Available from: http://www.water.ca.gov/iep/newsletters/2009/IEPNewsletter_Final2SUMMER-Fall2009%20.pdf
- Fisch K, Ivy J, Burton R, May B. In preparation. Fish hatchery or zoo population? Genetic analysis of the delta smelt captive breeding program. For submission to *Molecular Ecology* in June.

- Flagg TA, McAuley WC, Kline PA, Powell MS, Taki D, Gislason JC. 2004. Application of captive broodstocks to preservation of ESA-listed stocks of Pacific salmon: Redfish Lake Sockeye salmon case example. In: Nickum MJ, Mazik PM, Nickum JG, MacKinlay DD, editors. Propagated fish in resource management. American Fisheries Society Symposium 44. Bethesda (MD): American Fisheries Society. p. 387-400.
- Fraser DJ. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications* 1(4):535-586.
- Garza JC, Blankenship SM, Lemaire C, Charrier G. 2007. Genetic population structure of Chinook salmon (*Oncorhynchus tshawytscha*) in California's Central Valley. Draft final report for CALFED Project "Comprehensive evaluation of population structure and diversity for Central Valley Chinook salmon." Santa Cruz (CA): NOAA Southwest Fisheries Science Center p 82.
- George AL, Kuhajda BR, Williams JD, Cantrell MA, Rakes PL, Shute JR. 2009. Guidelines for propagation and translocation for freshwater fish conservation. *Fisheries* 34(11):529-545.
- Goldsworthy CA, Bettoli PW. 2006. Growth, body condition, reproduction and survival of stocked Barrens topminnows, *Fundulus julisia* (*Fundulidae*). *American Midland Naturalist* 156(2):331-343.
- Goodman D. 2005. Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. *Canadian Journal of Fisheries and Aquatic Sciences* 62(2):374-389.
- Hawkins SW, Tipping JM. 1999. Predation by juvenile hatchery salmonids on wild fall-run Chinook salmon fry in the Lewis River, Washington. *California Fish and Game* 96:124-129.
- Healey M. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In: Groot C, Margolis L, editors. Pacific salmon life history. Vancouver BC: UBC Press. p 313-396.
- Hedrick PW, Hedgecock D, Hamelberg S. 1995. Effective population-size in winter-run Chinook salmon. *Conservation Biology* 9(3):615-624.
- Hedrick PW, Hedgecock D, Hamelberg S, Croci SJ. 2000a. The impact of supplementation in winter-run Chinook salmon on effective population size. *Journal of Heredity* 91(2):112-116.
- Hedrick PW, Rashbrook VK, Hedgecock D. 2000b. Effective population size of winter-run chinook salmon based on microsatellite analysis of returning spawners. *Canadian Journal of Fisheries and Aquatic Sciences* 57(12):2368-2373.
- Henderson AP, Spidle AP, King TL. 2005. Genetic diversity, kinship analysis, and broodstock management of captive Atlantic sturgeon for population restoration. In: Nickum MJ, Mazik PM, Nickum JG, MacKinlay DD, editors. Propagated fish in resource management. Bethesda (MD): American Fisheries Society. p 621-634.
- Heublein JC, Kelly JT, Crocker CE, Klimley AP, Lindley ST. 2009: Migration of green sturgeon, *Acipenser medirostris*, in the Sacramento River. *Environmental Biology of Fishes* 84:245-258.
- Heppell SS. 2007. Elasticity analysis of green sturgeon life history. *Environmental Biology of Fishes* 79(3-4):357-368.
- Hilborn R. 1992. Hatcheries and the future of salmon in the Northwest. *Fisheries* 17(1):5-8.
- Hildebrand L, McLeod C, McKenzie S. 1999. Status and management of white sturgeon in the Columbia River in British Columbia, Canada: an overview. *Journal of Applied Ichthyology* 15:164-172.
- Hughes RM, Wildman RC, Gregory SV. 2005. Changes in fish assemblage structure in the main-stem Willamette River, Oregon. In: Rinne JN, Hughes RM, Calamusso B, editors. Historical changes in large river fish assemblages of the Americas. American Fisheries Society Symposium 45. Bethesda (MD): American Fisheries Society. p 75-98.
- Israel JA, Klimley AP. 2009. Life history conceptual model of North American green sturgeon (*Acipenser medirostris*). Sacramento (CA): California Department of Fish and Game Ecosystem Restoration Program. p. 49.

Israel JA, May BP. 2010. Indirect genetic estimates of breeding population size in the polyploid green sturgeon (*Acipenser medirostris*). *Molecular Ecology* 19:1058–1070.

Jones & Stokes, Inc. 2009. Draft hatchery and stocking program Environmental Impact Report/ Environmental Impact Statement. Prepared for the California Department of Fish and Game and U.S. Fish and Wildlife Service. (ICF J&S 00264.08) (SCH #2008082025). Sacramento (CA): Jones & Stokes, Inc.

Jonsson B, Jonsson N. 2006. Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish. *Ices Journal of Marine Science* 63(7):1162–1181.

Justice C, Pyper BJ, Beamesderfer RCP, Paragamian VL, Rust PJ, Neufeld MD, Ireland SC. 2009. Evidence of density- and size-dependent mortality in hatchery-reared juvenile white sturgeon (*Acipenser transmontanus*) in the Kootenai River. *Canadian Journal of Fisheries and Aquatic Sciences* 66(5):802–815.

Kimmerer WJ. 2008. Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento–San Joaquin Delta. *San Francisco Estuary and Watershed Science* [Internet]. Available from: <http://escholarship.org/uc/item/7v92h6fs>.

Korman J, Walters C. 2001. Nechako River white sturgeon recovery planning. Summary of stock assessment and Oct. 2–3, 2000 Workshop; 2001; BC Fisheries Victoria, BC. Available from: <http://wlapwww.gov.bc.ca/nor/fish/sturgeon/KormanReport.pdf>.

Kostow K. 2009. Factors that contribute to the ecological risks of salmon and steelhead hatchery programs and some mitigating strategies. *Reviews in Fish Biology and Fisheries* 19(1):9–31.

Kostow KE. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding. *Canadian Journal of Fisheries and Aquatic Sciences* 61(4):577–589.

Kostow KE, Zhou SJ. 2006. The effect of an introduced summer steelhead hatchery stock on the productivity of a wild winter steelhead population. *Transactions of the American Fisheries Society* 135(3):825–841.

Letcher BH, King TL. 1999. Targeted stock identification using multilocus genotype ‘familyprinting.’ *Fisheries Research* 43(1–3):99–111.

Levin PS, Williams JG. 2001. Interspecific effects of artificially propagated fish: an additional conservation risk for salmon. *Conservation Biology* 16(6):1581–1587.

Levin PS, Zabel RW, Williams JG. 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. *Proceedings of the Royal Society, London B* 268:1153–1158.

Lichatowich J. 1999. *Salmon without rivers*. Washington D.C.: Island Press. p. 336.

Lindley ST, Grimes C, Mohr MS, Peterson W, Stein J, Anderson JT, Botsford LW, Bottom DL, Busack CA, Collier TA and others. 2009. What caused the Sacramento River fall Chinook stock collapse?: Pre-publication report to the Pacific Fishery Management Council.

Lindley ST, Moser MM, Erickson DL, Belchik M, Welch DW, Rechiski E, Klimley AP, Kelly JT, Heublein JC. 2008. Marine migration of North American green sturgeon. *Transactions of the American Fisheries Society* 137:182–194.

Lindley ST, Schick RS, Agrawal A, Goslin M, Pearson T, Mora E, Anderson JJ, May BP, Greene S, Hanson C, and others. 2006. Historical population structure of Central Valley steelhead and its alteration by dams. *San Francisco Estuary Watershed Science* [Internet]. Available from: <http://escholarship.org/uc/item/1ss794fc>.

Lund J, Hanak E, Fleenor W, Howitt R, Mount J, Moyle P. 2007 *Envisioning futures for the Sacramento–San Joaquin Delta*. San Francisco (CA): Public Policy Institute of California. Available from: <http://www.ppic.org/main/publication.asp?i=671>

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

- Matern SA, Moyle PB, Pierce LC. 2002. Native and alien fishes in a California estuarine marsh: Twenty-one years of changing assemblages. *Transactions of the American Fisheries Society* 131(5):797–816.
- McClure MM, Utter FM, Baldwin C, Carmichael RW, Hassemer PF, Howell PJ, Spruell P, Cooney TD, Schaller HA, Petrosky CE. 2008. Evolutionary effects of alternative artificial propagation programs: implications for viability of endangered anadromous salmonids. *Evolutionary Applications* 1:356–375.
- Minckley WL. 1995. Translocation as a tool for conserving imperiled fishes—experiences in western United States. *Biological Conservation* 72(2):297–309.
- Minckley WL, Marsh PC, Deacon JE, Dowling TE, Hedrick PW, Matthews WJ, Mueller G. 2003. A conservation plan for native fishes of the Lower Colorado River. *Bioscience* 53(3):219–234.
- Mobrand LE, Barr J, Blankenship L, Campton DE, Evelyn TTP, Flagg TA, Mahnken CVW, Seeb LW, Seidel PR, Smoker WW, and others. 2005. Hatchery reform in Washington state: Principles and emerging issues. *Fisheries* 30(6):11–23.
- Moyle PB, Herbold B, Stevens DE, Miller LW. 1992. Life history and status of delta smelt in the Sacramento–San Joaquin Estuary, California. *Transactions of the American Fisheries Society* 121:67–77.
- Moyle PB, Israel JA, Purdy SE. 2008. Salmon, steelhead, and trout in California: status of an emblematic fauna. A report commissioned by California Trout Center for Watershed Sciences. Davis (CA): University of California, Davis. 316 p.
- Naish KA, Taylor III JE, Levin PS, Quinn TP, Winton JR, Huppert D, Hilborn R. 2008. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology* 53:61–194.
- Narum SR, Banks M, Beacham TD, Bellinger MR, Campbell MR, Dekoning J, Elz A, Guthrie CM, Kozfkay C, Miller KM, and others. 2008. Differentiating salmon populations at broad and fine geographical scales with microsatellites and single nucleotide polymorphisms. *Molecular Ecology* 17(15):3464–3477.
- Newman KB. 2008. Sample design-based methodology for estimating delta smelt abundance. *San Francisco Estuary and Watershed Science* [Internet]. Available from: <http://escholarship.org/uc/item/99p428z6>.
- Nickelson T. 2003. The influence of hatchery coho salmon (*Oncorhynchus kisutch*) on the productivity of wild coho salmon populations in Oregon coastal basins. *Canadian Journal of Fisheries and Aquatic Sciences* 60(9):1050–1056.
- [NMFS] National Marine Fisheries Service 2009. Biological opinion and conference opinion on the long-term operations of the Central Valley Project and State Water Project. Sacramento (CA): National Marine Fisheries Service. p 844.
- Osborne MJ, Benavides MA, Aló D, Turner TF. 2006. Genetic effects of hatchery propagation and rearing in the endangered Rio Grande silvery minnow, *Hybognathus amarus*. *Reviews in Fisheries Science* 14(1–2):127–138.
- Paragamian VL, Beamesderfer RCP, Ireland SC. 2005. Status, population dynamics, and future prospects of the endangered Kootenai river white sturgeon population with and without hatchery intervention. *Transactions of the American Fisheries Society* 134(2):518–532.
- Pearsons TN. 2010. Operating hatcheries within an ecosystem context using the adaptive stocking concept. *Fisheries* 35:23–31.
- Pearsons TN. 2008. Misconception, reality, and uncertainty about ecological interactions and risks between hatchery and wild salmonids. *Fisheries* 33(6):278–290.
- Pearsons TN, Fritts AL, Scott JL. 2007. The effects of hatchery domestication on competitive dominance of juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 64(5):803–812.

Poytress WR, Gruber JJ, Trachtenberg DA, Van Eenennaam JP. 2009. 2008 Upper Sacramento River green sturgeon spawning habitat and larval migration surveys. Unpublished report of the U.S. Fish and Wildlife Service to U.S. Bureau of Reclamation, Red Bluff, CA.

[RIST] Recovery Implementation Science Team. 2009. Hatchery reform science: A review of some applications of science to hatchery reform issues, April 9, 2009. Recovery Implementation Science Team, NOAA Fisheries–NWSFC. Available from: http://www.nwfsc.noaa.gov/trt/puget_docs/hatchery_report_april92009.pdf

Ryman N, Jorde PE, Laikre L. 1995. Supportive breeding and variance effective population size. *Conservation Biology* 9:1619–1628.

Schwartz MK, Luikart G, Waples RS. 2007. Genetic monitoring as a promising tool for conservation and management. *Trends in Ecology and Evolution* 22(1):25–33.

[SJRRP] San Joaquin River Restoration Program. 2010. Draft Fisheries Implementation Plan 2009–2010. Sacramento (CA): San Joaquin River Restoration Program Fisheries Management Work Group. 175 p.

Sommer T, Armor C, Baxter R, Breuer R, Brown L, Chotkowski M, Culberson S, Feyrer F, Gingras M, Herbold B, and others. 2007. The collapse of pelagic fishes in the Upper San Francisco Estuary. *Fisheries* 32(6):270–277.

Stockwell CA, Leberg PL. 2002. Ecological genetics and the translocation of native fishes: emerging experimental approaches. *Western North American Naturalist* 62(1):32–38.

Turner TF, Osborne MJ, Moyer GR, Benavides MA, Aló D. 2006. Life history and environmental variation interact to determine effective population to census size ratio. *Proceedings of the Royal Society B–Biological Sciences* 273(1605):3065–3073.

[USFWS] U.S. Fish and Wildlife Service. 1993. Endangered and threatened wildlife and plants: determination of threatened status for the delta smelt. *Federal Register* 58:2854–12863.

[USFWS] U.S. Fish and Wildlife Service. 2005. Upper basin pallid sturgeon propagation plan. Place?: U.S. Fish and Wildlife Service. 89 p.

[USFWS] U.S. Fish and Wildlife Service. 2008. Endangered Species Act consultation on the proposed coordinated operations of the Central Valley Project and State Water Project. Sacramento (CA): U.S. Fish and Wildlife Service, California and Nevada Region. 410 p.

[USFWS] U.S. Fish and Wildlife Service. 2009. Upper Sacramento River winter–run Chinook salmon carcass survey. Red Bluff (CA): U.S. Fish and Wildlife Service. p. 28.

Utter F, Epifanio J. 2002. Marine aquaculture: genetic potentialities and pitfalls. *Reviews in Fish Biology and Fisheries* 12(1):59–77.

Van Eenennaam JP, Linares–Casenave J, Muguet J, Doroshov SI. 2008. Induced spawning, artificial fertilization and egg incubation techniques for green sturgeon. *North American Journal of Fisheries Management* 70:434–445.

Waples RS, Drake J. 2004. Risk–benefit considerations for marine stock enhancement: a Pacific salmon perspective. In: Leber KM, Kitada S, Blankenship HL, Svasand T, editors. *Stock enhancement and sea ranching: developments, pitfalls, and opportunities*. Oxford UK: Blackwell. p. 260–306.

Waples RS, Ford MJ, Schmitt D. 2007. Empirical results of salmon supplementation in the Northeast Pacific: a preliminary assessment. In: Bert TM, editor. *Ecological and genetic implications of aquaculture activities*. p. 383–403.

Washington PM, Koziol AM. 1993. Overview of the interactions and environmental impacts of hatchery practices on natural and artificial stocks of salmonids. *Fisheries Research* 18(1–2):105–122.

Williams JG. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. *San Francisco Estuary and Watershed Science* [Internet]. Available from: <http://escholarship.org/uc/item/21v9x1t7>.

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Williamson KS, May B. 2005. Homogenization of fall-run Chinook salmon gene pools in the Central Valley of California, USA. *North American Journal of Fisheries Management* 25(3):993–1009.

Yoshiyama RM, Fisher FF, Moyle PB. 1998. Historical abundance and decline of chinook salmon in the Central Valley region of California. *North American Journal of Fisheries Management* 18:487–521.