Biological Conservation xxx (xxxx) xxx-xxx

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: http://ees.elsevier.com

Perspective

Wild at heart: Programs to diminish negative ecological and evolutionary effects of conservation hatcheries

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ARTICLE INFO

Keywords
Adaptation
Captive breeding
Conservation genetics
Selection

ABSTRACT

Hatchery programs are critical for conservation and management of many imperiled fishes. Most traditional aquaculture programs negatively affect ecological performance, genetic, and phenotypic diversity of hatchery-origin fish compared with wild counterparts. Here, we synthesize outcomes of three conservation programs aimed at enhancing ‘wildness’. Each program focuses on a different species: lake sturgeon, razorback sucker, and Rio Grande silvery minnow. These species differ in key life history traits including size and age at sexual maturity, reproductive and migratory behavior, and habitat requirements. Threats to persistence of the focal taxa, however, exemplify common pressures experienced by freshwater fishes worldwide. Conservation hatchery programs for lake sturgeon, razorback sucker, and Rio Grande silvery minnow capitalize on natural spawning in the wild followed by collections of wild-fertilized eggs/larvae for hatchery rearing. Individuals are repatriated to the wild after rearing to body sizes less susceptible to mortality. Protocols include collections of eggs or larvae across the entire spawning period and at appropriate geographic scales to maximize retention of genetic diversity and, to increase the likelihood of preserving variation for heritable life history traits. Using direct and indirect evidence we show that hatchery programs that allow individuals to fulfill parts of the life-cycle in their native habitats can be conducted without compromising genetic diversity. Adoption of similar strategies in other imperiled fishes would improve understanding of species life history, and provide an incentive to protect native habitats so they may eventually support self-sustaining populations.

1. Introduction

Freshwater ecosystems worldwide have lost proportionally more species and habitats than oceanic and terrestrial systems (Sala et al., 2001; Millennium Ecosystem Assessment, 2005). Biodiversity losses coincide with the development of impoundments and dams, water extraction to meet surging global demand for freshwater (*e.g.*, Malmqvist and Rundle, 2002; Jelks et al., 2008), and transformation of adjacent riparian habitats for municipal, agriculture and industry needs (Esselman et al., 2011). Attempts to stem biodiversity loss are especially challenging in freshwaters because necessary conservation actions are usually incompatible with competing priorities including maintaining engineered systems to meet human water needs (*e.g.* Richter et al., 2003) or providing support for non-native commercial and recreational fisheries (*e.g.*, Rochard et al., 1990; Clarkson et al., 2005). Other challenges confronted by freshwater and anadromous fishes include reduced or absent spawning habitat, low spawner abundance, and high early life mortality (*e.g.*, Moyle and Leidy, 1992; Clarkson and Childs, 2000).

Artificial breeding and rearing programs in hatcheries are now widely employed in fish conservation and recovery programs, ostensibly to improve probabilities of species or population persistence. Hatcheries also serve as sources for restocking in the event of extirpation or extinction in the wild. Unfortunately, traditional hatchery culture practices exert negative effects on performance and genetic diversity (*e.g.*, Allendorf and Phelps, 1980; Frost et al., 2006) of hatchery-origin fish (*e.g.*, Ford, 2002; Lynch and O'Hely, 2001) when compared to wild fish (Araki et al., 2007; Araki et al., 2008). For example, release of hatchery-origin individuals may alter evolutionary trajectories and long-term viability of populations or species (*e.g.* McClure et al., 2008; Araki and Schmidt, 2010; Williamson et al., 2010) and may contribute to extirpation of wild populations (*e.g.*, Quiñones et al., 2014). Traditional programs have other well-documented negative effects including: (1) domestication selection encom-

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https://doi.org/10.1016/j.biocon.2020.108768
Received 25 March 2020; Received in revised form 27 July 2020; Accepted 21 August 2020

passing both adaptation to hatchery environments and relaxation of selection that would otherwise occur in the wild (*e.g.*, Utter, 1998; Waples, 1999; Ford, 2002; Heath et al., 2003; Christie et al., 2012), (2) outbreeding depression (*e.g.*, Goldberg et al., 2005), (3) homogenization of population structure (*e.g.*, McClure et al., 2008), and (4) diminished effective population size, loss of genetic diversity, and increased (average) relatedness among captive individuals (Ryman and Laikre, 1991; Bartron et al., 2018).

Substantial investment has been made to reform conservation hatchery practices in response to these risks (Mobrand et al., 2005; Fisch et al., 2015; Paquet et al., 2011), but efforts are mostly restricted to commercially or culturally important taxa like salmonid fishes. In Pacific salmon (*Oncorhynchus* sp.) for example, hatchery operations have been modified to maintain adaptive variation for traits suited to changing environmental conditions, to improve survival of hatchery-produced offspring, and thereby increase success of supplementation programs. Reformed programs implement rearing and feeding regimes that more closely reflect natural conditions (*e.g.* Näslund and Johnsson, 2016), use natal waters to improve homing fidelity (*e.g.* Dittman et al., 2015), and integrate wild or local broodstock into hatchery programs (*e.g.* Ward, 2006; Mobrand et al., 2005). Nonetheless, hatchery activities impact every stage of the life cycle until the organism is repatriated into the wild (*e.g.* Berejikian, 1995; Petersson et al., 1996; Araki et al., 2008). To mitigate risks intrinsic to hatchery breeding, programs for anadromous salmon have also explored use and subsequent performance of captive reared early life-stages collected from wild spawning events (*e.g.*, Berejikian et al., 1997, 1999; Berejikian et al., 2001; Stark et al., 2014; Venditti et al., 2013; Moore et al., 2012). These studies provide valuable information but salmonids do not capture the full scope of life-histories exhibited by fishes in general.

The scope of variability in fish life history traits can be characterized by three end points (Fig. 1) defined by aspects of growth, survival, maturation, and reproduction (Winemiller and Rose, 1992). Pacific salmon represent a special case of the ‘equilibrium’ strategy and are characterized by rapid growth, relatively large energetic investment per offspring (egg size), intensive nest site selection and defense, and long early development times as larvae remain in the nest for months before emerging (Quinn, 2018). Equilibrium strategies are optimal when environmental conditions are stable. Other fishes are ‘periodic’ strategists characterized by sexual maturation at larger body size and age, enormous clutches but small egg size, little or no parental care, and high juvenile mortality. This life history is optimal when environmental conditions that promote growth and survival of offspring are predictable (*e.g.*, seasonal) and recur at frequencies shorter than the average life span of adults (Winemiller and Rose, 1992). In contrast, an ‘opportunistic’ end point is favored when environments are variable and unpredictable. Species exhibiting this life history are characterized by early maturation at small body size, short life span, and relatively small clutch sizes. Many freshwater fish species exhibit periodic, opportunistic, or intermediate life histories that differ substantially from those exhibited by most salmon.

In this paper, we compare conservation hatchery programs for fish species that occupy portions of life-history space not occupied by salmonids. These species were chosen because wild populations have been augmented for almost 20 years with fish reared in captivity, and genetic monitoring was implemented as part of each species' recovery program. Some conservation programs for these species promote ‘wildness’ by incorporating large numbers of individuals (eggs/larvae or adults) exposed to natural conditions at key points in their life cycle into annual hatchery activities. We illustrate strategies and outcomes through comparative study of three freshwater fishes, lake sturgeon (*Acipenser fulvescens*, Acipenseridae), razorback sucker (*Xyrauchen texanus*, Catostomidae), and Rio Grande silvery minnow (*Hybognathus amarus*, Cyprinidae). These species and particular conservation programs are highlighted because (i) each is the subject of long-term demographic and genetic research that informs science-based culture practices and adaptive management, (ii) they represent periodic and opportunistic life histories (Winemiller and Rose, 1993; Winemiller, 2005) and, (iii) each species poses different conservation challenges that mirror those experienced by freshwater fish programs worldwide. We use direct and indirect evidence to examine if genetic diversity has been maintained in fish produced using these strategies and whether they survive in the wild and exhibit traits equivalent (*e.g.*,

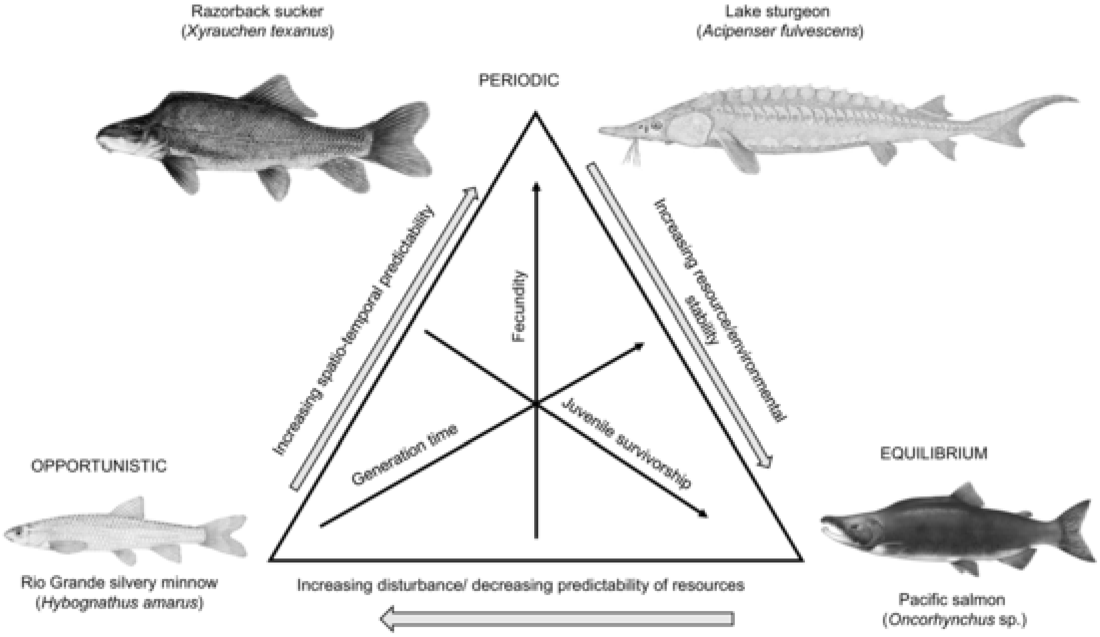

Fig. 1. The life history continuum model proposed by Winemiller and Rose (1992) and Winemiller (2005) that describes the trade-offs between fecundity, generation time and juvenile survivorship between the three end-point strategies: equilibrium (*e.g.*, salmonids), opportunistic, and periodic. The arrows indicate increasing investment. Lake sturgeon image credit: Freshwater and Marine Image Bank University of Washington; Rio Grande silvery minnow and razorback sucker illustrations used with permission of W. H. Brandenburg.

spawning timing, behavior) to wild counterparts. Strategies and protocols outlined here could be employed more broadly where hatcheries are necessary to enhance the likelihood of long-term population and species' persistence.

2. Case studies

2.1. Lake sturgeon

Historical and current impediments to restoration - Lake sturgeon is a long-lived, iteroparous, riverine-spawning teleost belonging to the family Acipenseridae (Houston, 1987). Longevity, high fecundity, and extensive mortality of eggs and larvae are characteristic of fishes that occupy the 'periodic' endpoint of the life history spectrum. Lake sturgeon distribution is centered around the Great Lakes in southern and central Canada and the north-central portions of the United States (Scott and Crossman, 1973). Historically, lake sturgeons were highly abundant, but current distribution and abundance is likely $<1\%$ of historical levels (Hay-Chmielewski and Whelan, 1997). Lake sturgeon is a threatened species in Michigan, a species of conservation concern in the U.S. and Canada, is categorized as a species at risk (COSEWIC, 2017).

Lake sturgeon is sensitive to poor water quality, river obstruction and altered stream flow regimes caused by dams (Auer, 1996; Holey et al., 2000; Haxton and Findlay, 2009). Adults migrate from lakes to rivers to spawn and require clean rock substrate for spawning in high gradient river reaches (Peterson et al., 2007). Many historically important spawning areas with these conditions have been blocked or degraded due to the effects of dams (Daugherty et al., 2009; Coscarelli et al., 2011). Recently, U.S. federal regulations of hydroelectric dam operations were established to control undesirable variability (*e.g.*, hydropeaking) in stream flow regimes. The passage of the Clean Water Act in 1973 has also led to improved water quality throughout the species' range. Harvest regulations have been widely initiated, greatly reducing adult mortality and bolstering population size (Holey et al., 2000; Hay-Chmielewski and Whelan, 1997). Nonetheless, natural recruitment in most populations is below levels necessary to sustain populations, in part because dams still impede fish passage and preclude spawning in historically important areas (Birstein, 1993; Nilo et al., 1997; Peterson et al., 2007).

2.1.1. Reproductive ecology

Lake sturgeon is characterized by a late maturation time (10–25 years depending on sex and location; Peterson et al., 2007; Bruch et al., 2016) (Table 1). Inter-spawning intervals vary, with females spawning every 3–4 years while males spawn more frequently (1–2 years, Forsythe et al., 2012a). Longevity and iteroparity buffer the species from losses of genetic diversity due to low population numbers. For example, DeHaan et al. (2006) found no relationship between current estimated population census size and levels of genetic diversity. Long generation times mean that only a few generations have elapsed since populations were severely reduced in the late 1800s and early 1900s. However, persistent small population sizes coupled with low levels of recruitment will continue to erode levels of genetic diversity and increase levels of inbreeding (Schueller and Hayes, 2010).

Lake sturgeon naturally exhibit aggregate mating behavior (Bruch and Binkowski, 2002), where sinking demersal eggs and sperm are released by males and females over rocks and gravel without nest preparation or post-ovulatory parental care. Upon contact with water, small (~2.5 mm) eggs become adhered to bottom substrates. Female lake sturgeon is a highly fecund fish, with egg numbers related to body weight (11,000/kg; Bruch and Binkowski, 2002). Female reproductive success is influenced by operational sex ratio (higher when male-skewed), water temperature, and stream flow (Dammerman et al., 2019).

There is extremely high mortality at the egg and larval stages due to predation and arrested development during incubation (Forsythe et al., 2013; Fujimoto et al., 2017) so despite the species' high reproductive potential, there is limited natural recruitment beyond the first year of life. Depensatory effects of low spawning numbers include depressed fertilization rates and alteration of retention times on spawning areas (Duong et al., 2013; Dammerman et al., 2019). Dams, climate change, and associated variability in flow regimes have altered normal river discharge and thermal regimes resulting in 'ecological and evolutionary traps' (Schlaepfer et al., 2002). Ecological and evolutionary traps occur when sudden changes are made to habitats so formerly reliable cues are no longer associated adaptive consequences. For example, environmental cues including increasing water temperature and decreasing stream discharge levels that have been shown to be tied to initiation of spawning in lake sturgeon (Forsythe et al., 2012a) are increasingly temporally variable within a spawning season, and are less likely to elicit an adaptive reproductive response regarding where and when to spawn (Dammerman et al., 2015, 2016).

Due to low levels of natural recruitment, hatchery supplementation is widely embraced as a viable strategy for lake sturgeon recovery. Restoration objectives for lake sturgeon include development of science-based hatchery programs that (1) assist conservation efforts of wild populations, and (2) support or restore sustainable fisheries. Successes of lake sturgeon stocking programs are partly dependent on aquaculture practices that simultaneously improve early life survival and encourage homing of adults to natal streams to spawn. Logistical constraints imposed by large body size of sturgeon, low wild abundance (Holey et al., 2000) and other life-history characteristics preclude maintenance of a captive broodstock (Bruch and Binkowski, 2002). In contrast, captive broodstocks are widely used to supply sturgeon for harvest in Europe (Chebanov et al., 2011) and for some conservation programs (*e.g.*, Atlantic sturgeon, St. Pierre et al., 2006; Henderson et al., 2005; pallid sturgeon, Heist et al., 2009). Captive broodstocks offer flexibility as substantial numbers of non-reproductive individuals can be collected, and they permit genetic screening to design orchestrated matings (*e.g.*, Atlantic salmon [*Salmo salar*], Herbinger et al., 2006). However, this approach is not used for lake sturgeon, nor is it typically employed for conservation hatchery programs for sturgeon, due to cost and time limitations. Given concerns regarding lake sturgeon imprinting and their return to stocked rivers when mature, streamside rearing facilities were developed (Holtgren et al., 2007). These facilities use water from intended release streams. The high levels of spatial genetic structure observed for remnant Great Lakes populations (DeHaan et al., 2006) suggests spawning adults are philopatric to natal streams. Therefore, as a precautionary procedure, managers rear eggs and/or larvae to increase the probability of hatchery-reared individuals returning to natal rivers when mature (Crossman et al., 2011a, 2011b).

2.1.2. Incorporating wildness into hatchery and supplementation activities

Gametes collected from wild-caught adults spawned in the hatchery are a fundamental component of traditional hatchery lake sturgeon conservation programs (Crossman et al., 2011a), and more recently to population streamside hatchery facilities on Great Lakes tributaries. Managers prioritize use of local gamete sources; however, breeding population numbers may be low during any given year so few adults may contribute to an entire year class of offspring. Many thousands of eggs can often be collected from each female however, obtaining large numbers of actively spawning females can be problematic. Hence, sole reliance on hatchery production using direct gamete take would result in low annual effective population sizes for cohorts produced and ultimately compromise genetic diversity. Furthermore, unless adult lake

Table 1
Summary of aspects of species biology, threats and management actions for lake sturgeon, razorback sucker and Rio Grande silvery minnow.

Species	Longevity	Sexual maturity	Adult size	Fecundity (per year)	Reproduction	Threats	Management actions
Lake sturgeon	100 years	10–25 years	1–2.5 m	∼100,000-700,000	Demersal adhesive eggs	Habitat degradation or inaccessibility of spawning sites	
	[1]	Varies by sex and location [2]	(TL) [1]	Or 11,000/kg [3]	Variable inter-		Use of naturally produced larvae
					Spawning interval		
							Streamside rearing of larvae in natal water Low density
					Aggregate spawning Male biased OSR [3, 4]	Altered flow regime	Low density [5, 6]
						Fragmentation [1, 2]	
Razorback sucker	> 44 years [7]	3–4 yrs. (♀)	< 1 m	75,000–200,000 [8, 9]	Adhesive eggs [12]	Predation by non-native species limits recruitment [11]	Collection of wild-spawned larvae for hatchery rearing [13]
		1 yr (♂) [10]					
					Aggregate spawning [12]		Rearing of juveniles in protected backwaters [13]
Rio Grande silvery minnow	< 2 years [14]	1 yr (♀, ♂)	< 90 mm TL	∼2000–10,000 [15]	Semi-buoyant, non-adhesive eggs [16]	Altered flow regime	Collection of eggs from wild spawning for hatchery rearing [17]
					Aggregate spawner	Channel drying, Fragmentation	Supportive breeding using group spawning [17] Determination of stocking densities based on *CPUE* and target densities

[1] Bruch et al. (2016), [2] Peterson et al. (2007), [3] Bruch and Binkowski (2002), [4] Dammerman et al. (2019), [5] Holtgren et al. (2007), [6] Crossman et al. (2011a), [7] McCarthy and Minckley (1987), [8] McAda and Wydoski (1980), [9] Minckley (1983), [10] Mueller (2006), [11] Marsh and Langhorst (1988), [12] Minckley (1973), [13] reviewed in Marsh et al. (2015), [14] Horwitz et al. (2018), [15] Caldwell et al. (2019), [16] Platania and Altenbach (1998), [17] U.S. Fish and Wildlife Service (2018).

sturgeon is hormonally induced to extrude gametes, gametes must be collected from actively spawning individuals. Except in rare instances such as the Black River population in Michigan where nearly all adults have been previously captured and genotyped, marker assisted analyses (*e.g.*, Herbinger et al., 2006) are not a viable alternative to selecting pairs of individuals to spawn as a means of avoiding crossing related individuals.

Data show that samples taken from naturally dispersing larvae are representative of a large portion of the adult spawning population (Crossman et al., 2011a; Duong et al., 2013, Dammerman et al., 2019; Fig. S1). In support of lake sturgeon stream-side hatchery operations, the preferred strategy is to collect wild-produced larvae during the larval dispersal period (Fig. 2), rear them until the fall fingerling stage (∼140 mm), and release them into the wild population (Table 2). In the Black River (Cheboygan Co. Michigan, USA) over 250 adults

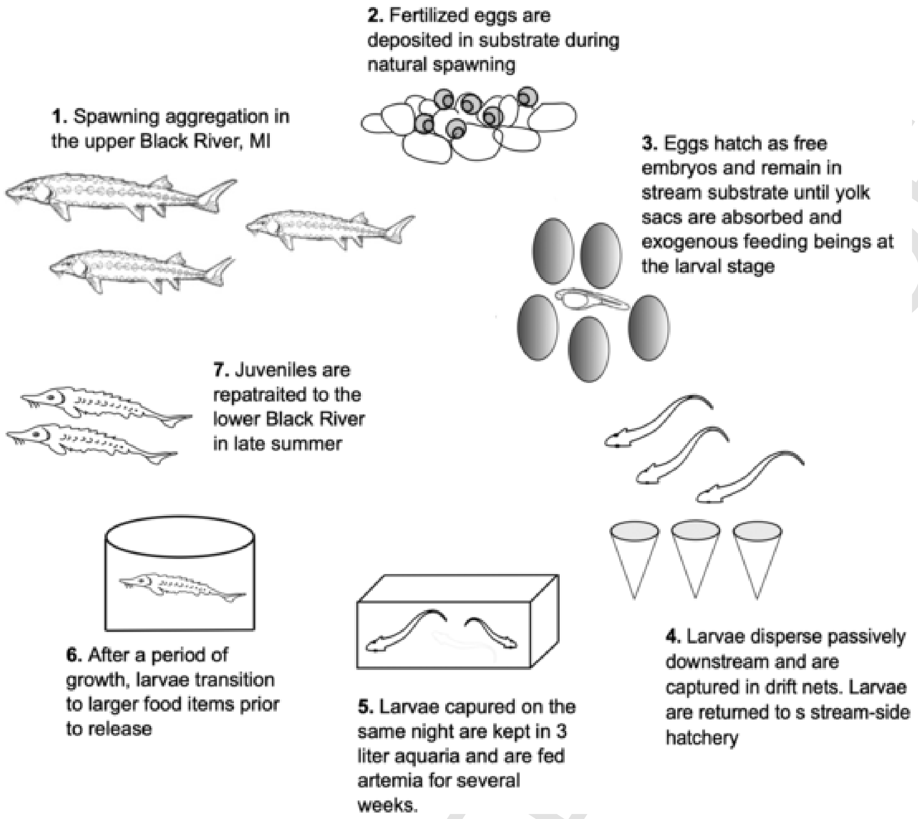

Fig. 2. Schematic depicting the integration of hatcheries into the life cycle of lake sturgeon. Adults reside in Black Lake (MI). Adults will migrate ~7 km to their spawning area covering ~2 km of stream. 1) Adults spawn naturally (Dammerman et al., 2019) and (2) eggs are deposited on stream substrate. 3) At hatch, free embryos will immediately burrow into the stream substrate and will remain in the substrate until they absorb their yolk sac and develop sensory ability. 4) At the onset of exogenous feeding, larvae leave the spawning areas and disperse passively downstream to find suitable foraging habitats. Larvae are intercepted in D-frame drift nets. Captured larvae are returned to a streamside hatchery on the upper Black River. 5) Larvae are placed in three liter aquaria and fed live artemia larvae. 6) After several weeks, larvae are transferred to larger containers. 7) Individuals are released in proportion to nightly representation in the drift back into lower regions of the Black River at the end of the summer. Fin biopsy samples are collected from each released individual to be genotyped to identify male and female parents., Illustrations provided by Lydia Wassink.

typically spawn annually (Pledger et al., 2013) and the number of larvae captured in D-frame drift nets has varied from 437 to 16,417 between 2001 and 2010 (Duong et al., 2013). Individuals are reared under ambient temperature conditions in water with odorants and other environmental cues from the natal stream. Streamside hatcheries using natal water also provide natural daily and seasonal variation in water chemistry (Crossman et al., 2011a). Analyses conducted by Crossman et al. (2011a, 2011b) evaluated the effects of hatchery culture location on measures of genetic variability and survival following release. Results demonstrated that survival and growth of larval sturgeon reared in streamside facilities were significantly higher than those reared in traditional hatcheries (Crossman et al., 2011b). Crossman et al. (2011a) also evaluated different methods of gamete/larval collections on summary measures of genetic diversity including heterozygosity and coancestry. Measures of genetic diversity (heterozygosity, allelic diversity) were significantly higher and coancestry (*i.e.*, relatedness) was reduced in larvae collected from the stream when compared to offspring produced from direct gamete takes or from naturally produced eggs collected from stream substrate. Larval lake sturgeon body size (Dammerman et al., 2014) and growth (Dammerman et al., 2015) have relatively high heritability ($h^2 = 0.42$). Large G*E (genetic or family by environment [*e.g.*, temperature]) interactions suggest that maintaining high levels of genetic diversity in offspring produced each year is important because aquatic environmental conditions will differentially affect offspring of different families, thereby decreasing levels of genetic diversity (*via* variable survival among members of different families) (Figs. 3 and 4).

2.2. Razorback sucker

2.2.1. Historical and current impediments to restoration

Razorback sucker is a large (> 750 mm total length [TL]), long-lived (> 44 years; McCarthy and Minckley, 1987) member of the family Catostomidae. The species occupies an intermediate life-history space between periodic and opportunistic endpoints. It is endemic to the Colorado River drainage of the western United States (Minckley, 1991; Minckley and Marsh, 2009; Bestgen et al., in press). Razorback sucker were once abundant in large rivers and associated floodplains throughout the drainage (Minckley et al., 2003; Marsh et al., 2015). Human-induced impacts including alterations to the natural flow regime and introduction of non-native fishes that prey on larvae, juveniles, and adults have resulted in dramatic reduction in numbers of individuals throughout the basin (Minckley, 1991; Marsh et al., 2003; Minckley and Marsh, 2009; Marsh et al., 2015). Small, remnant populations persist in mainstream reservoirs of Lakes Mead, Mohave, and Powell in addition to populations in the Colorado River in Colorado, and the Green and Yampa rivers in Colorado and Utah (Minckley, 1983; Bestgen et al., in press). Following construction of reservoirs, most populations of razorback sucker generally followed a declining demographic trajectory to local extirpation. Shortly after reservoirs filled, adults produced a few strong year classes leading to temporary population growth. As non-native fish populations expanded into these reservoirs and preyed upon larvae (Marsh and Langhorst, 1988), razorback sucker recruitment dwindled and ultimately ceased entirely (Marsh et al., 2003; Marsh et al., 2015). Remnant razor-

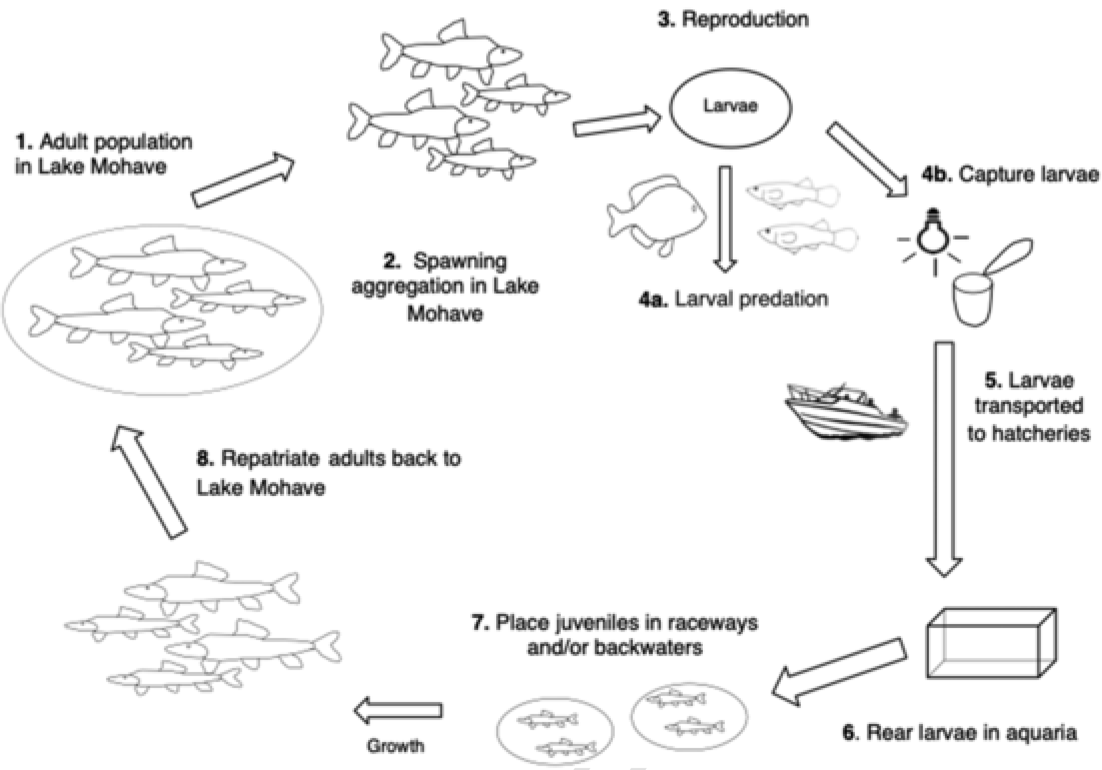

Fig. 3. Schematic depicting the integration of hatcheries into the life-cycle of razorback sucker. Adults reside in Lake Mohave (1), where they aggregate and spawn naturally in the winter and early spring (2), produce larvae (3) most larvae are eliminated by centrarchid and poecilid predators (4a), others are harvested (4b) and transported to the hatchery (5). In the hatchery larvae are reared in aquaria (6) until they are large enough to be placed in backwaters or hatchery raceways (7). Once they are large enough, these adults are repatriated back into Lake Mohave (8).

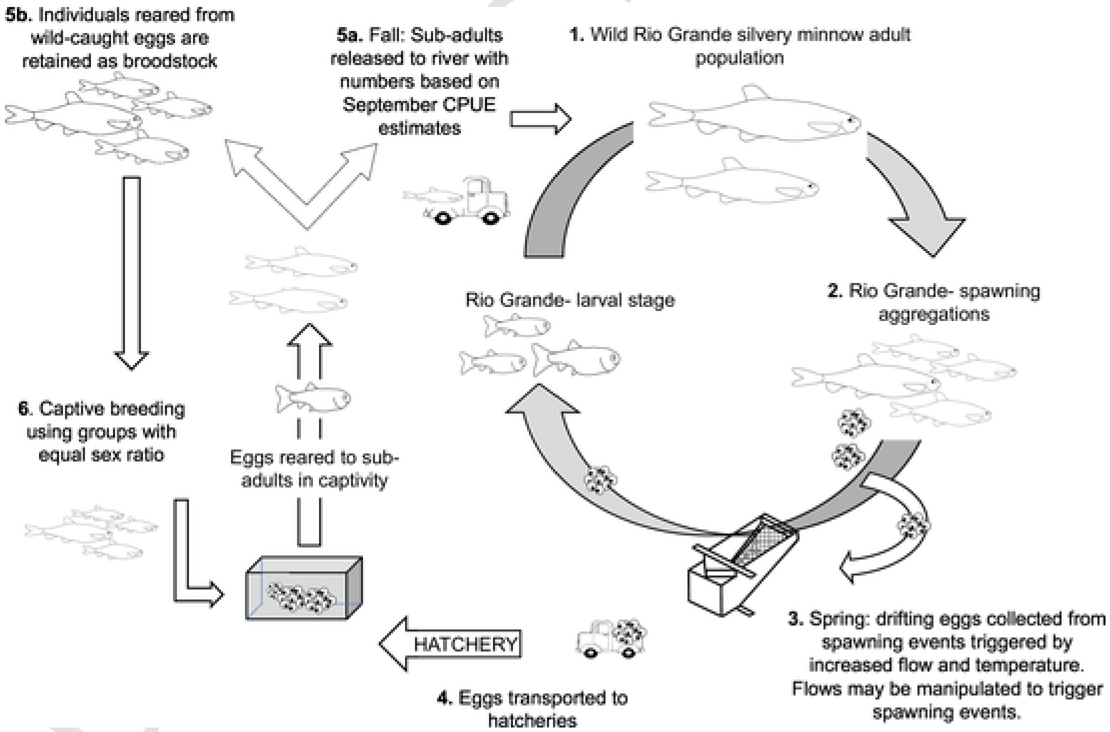

Fig. 4. Schematic depicting the integration of hatchery practices into the life-cycle of Rio Grande silvery minnow. 1) The wild population resides in the middle Rio Grande, New Mexico, (2) Natural spawning occurs in the spring and early summer and is associated with elevated stream flow from snowmelt runoff/rainstorm events and increases in water temperature, (3) Females release non-adhesive semi-buoyant pelagic eggs into the water column. A portion of drifting eggs are collected using Moore egg collectors and all other eggs are left in the river to develop and recruit if environmental conditions are favorable, (4) Eggs are transported to hatchery facilities where they are reared in tanks or outdoor ponds, (5a) Sub-adults are released to the river in November and (5b) some fish are retained to serve as future broodstock, (6) In years where insufficient numbers of eggs are collected to serve as broodstock and to supplement the riverine population, captive spawning utilizing a group spawning design is used to meet the demands of the supplementation program and to prevent extinction.

Table 2
Summary of management goals, key innovations and outcomes for lake sturgeon, razorback sucker and Rio Grande silvery minnow.

Species	Management goals	Key innovations	Outcomes
Lake sturgeon	Maintain a genetically diverse adult spawning population in Black Lake and adjoining lakes in the Cheboygan River drainage	Wild-caught drifting larvae are collected, reared to the late summer juvenile stage in streamside hatcheries, and released to the river.	Collections of naturally produced eggs/dispersing larvae following hatch result in significantly higher proportions of spawning adults contributing to annual hatchery production relative to direct gamete takes, thereby maintaining high levels of genetic diversity in juveniles released.
	Increase adult spawner abundance.	No intervention in mate choice, spawning behavior – captive rearing for 60–90 days from larval to juvenile stages.	Streamside facilities that use natal water sources result in higher offspring survival than traditional hatcheries and higher probabilities of natal imprinting.
Razorback sucker	Maintain a genetically diverse population in Lake Mohave while trying to expand the population.	Wild-caught larvae are collected from natural spawning events in Lake Mohave, reared to adult stages in captivity, and released back to the lake at sizes that reduce mortality of adults.	Genetic diversity has been maintained over >20-year genetic monitoring effort.
		There is no intervention in mate choice, spawning behavior or spawning site selection. Larvae are reared from larval to maturing adult stages in captivity.	Recruitment is facilitated by rearing without predators and survival is improved by release at larger sizes
Rio Grande silvery minnow	Maintain a genetically diverse population in the middle Rio Grande	Initial captive breeding population was established from large numbers of eggs (*i.e.*, hundreds of thousands) collected from the riverine spawning population.	Genetic diversity has been maintained over 20-year genetic monitoring effort and the middle Rio Grande population has not been extirpated.
	Maintain a genetically diverse refuge population to counter catastrophic demographic losses prior to spawning including absence of sufficient spring flows or recruitment failure due to extensive river drying.	Wild-caught drifting eggs are collected, reared to adult stages, and released to the river.	
		Water managers may intervene to provide flows that initiate spawning and facilitate egg collection	

Table 2 (*Continued*)

Species	Management goals	Key innovations	Outcomes
		No intervention in mate choice or spawning behavior. Captive rearing from egg/larval to subadult stages.	

back sucker populations persisted until adults grew old and perished, and local extirpation ensued. In more recent years, introduction of large predatory fishes for sport fishing (*e.g.*, largemouth bass [*Micropterus salmoides*], striped bass [*Morone saxatilis*]) has negatively impacted adult populations, hastening the demise of razorback sucker populations. Together these issues resulted in listing of razorback sucker as an endangered species (U.S. Fish and Wildlife Service [USFWS], 1991), and all extant populations are currently maintained by stocking.

2.2.2. Reproductive ecology

The biology of razorback sucker has been studied extensively (reviewed by Minckley, 1991; Minckley and Marsh, 2009). Briefly, males typically achieve sexual maturity at 2–3 years and females generally become reproductive at ages 3–5. Female razorback is a moderately fecund fish, with larger individuals capable of producing >100,000 eggs per year. Like lake sturgeon, iteroparity and long lifespan of razorback sucker buffers against loss of genetic diversity because each individual has multiple opportunities to successfully spawn.

Individual movement can range from 10 to >100 km annually, including movements to multiple spawning areas within a season (Tyus and Karp, 1990; Mueller et al., 2000; Karam et al., 2008; Durst and Francis, 2016). High movement propensity is consistent with high levels of gene flow observed among spawning areas (Dowling et al., 1996, 2012). Prior to dam construction, razorback suckers were observed migrating up rivers in early spring, presumably to spawn. In Lake Mohave, this species tends to reproduce in shallow areas (<5 m) over cobble (reviewed in Minckley, 1991). Large groups of males are found in the shallower inshore habitats, with aggregations of females found in deeper offshore waters. Sampling of spawning areas found twice as many males as females (Minckley, 1983). Individual receptive females move inshore to spawn, typically accompanied by two or more males.

Various management strategies have been adopted for conservation of razorback sucker with initial efforts focused on traditional hatchery production practices, with thousands of larvae produced and stocked into formerly occupied habitats (Marsh and Brooks, 1989; Minckley, 1991; Jahrke and Clark, 1999). Modifications of this approach are still used in certain areas, but these efforts have been largely unsuccessful and have not achieved self-sustaining populations. Unfortunately, predation of sucker larvae by nonnative fishes is intense and is likely the most significant contributor to recruitment failure (Marsh and Langhorst, 1988; Ehlo et al., 2017).

2.2.3. Incorporating wildness into hatchery and supplementation activities

Unlike other remnant populations, the Lake Mohave (a main stem reservoir in Arizona and Nevada) population remained large (>60,000 individuals) into the late 1980s, and thus became a focal point for study and conservation actions in the lower Colorado River basin (Minckley, 1983; Minckley, 1991). In the early 1990s, managers evaluated several conservation strategies (Marsh et al., 2015); ultimately deciding to use naturally-produced larvae to repatriate Lake Mohave. Throughout the spawning season, larvae are captured from five major spawning aggregations found in different parts of the lake. Upon capture, larvae are reared in aquaria in the hatchery and subsequently released into raceways and/or backwater ponds until they have achieved a size presumed sufficient to escape predation. Subsequently, they are repatriated to the lake (Mueller, 1995; Minckley et al., 2003) to complete their life cycle. This approach was selected to maximize the number of spawning adults contributing larvae, thereby maintaining genetic variation for future generations. During the >25-year period through 2019, almost a million larvae have been harvested, and >227,282 of these fish have been stocked back into Lake Mohave. Annual larval harvest averaged 37,832 individuals per year, ranging from 11,833 in 1994 (first year of sampling) to 108,877 in 1997. The number of larvae sampled was much higher earlier in the program (622,168 prior to 2007 compared to 361,461 subsequently), and earliest stockings were comprised of relatively small individuals that were apparently lost to predation (Marsh et al., 2015). In recent years, the size of stocked fish has increased which has improved long-term survival (Kesner et al., 2016) and resulted in maintenance of a small population comprising thousands of individuals in Lake Mohave (Burgad et al., 2019).

Genetic data indicates that using naturally produced larvae as a source of repatriates has successfully preserved genetic diversity (Dowling et al., 2005; Turner et al., 2007; Dowling et al., 2014). Analyses of patterns of mtDNA variation (*e.g.*, haplotypic richness, gene diversity) in larvae within and among four regions detected temporal and spatial differences. Observed differences were likely attributable to the smaller number of individuals contributing larvae to these local breeding aggregations resulting in differences in haplotype frequencies among temporal and spatial breeding aggregations. There may also be higher levels of relatedness within such groups. In contrast, analyses of regional and annual differences (pooling all samples by location and/or year) did not detect differences among spawning aggregations or across years (Dowling et al., 2005). Likewise, examination of larvae, repatriates, and wild adults did not identify genetic differences among these groups. This data indicated that using naturally produced larvae successfully maintained mtDNA variation over the initial phase of the repatriation project. Dowling et al. (2014) extended analysis of larval individuals through 2011 to assess genetic variation (*e.g.*, allelic richness, heterozygosity) at 14 microsatellite loci and mtDNA from all years. Neither set of genetic markers detected differences in patterns of genetic variation (Fig. S1B) among years. Carson et al. (2016) identified similar patterns of mtDNA and microsatellite variation in repatriates as observed in larvae, and did not identify differences among stocking cohorts of repatriates and wild adults. Therefore, extensive long-term genetic monitoring indicates that rearing wild-caught larvae in predator-free environments has been highly successful at maintaining genetic variation found in the original wild adult population in Lake Mohave.

3. Rio Grande silvery minnow

3.1. Historical and current impediments to restoration

Rio Grande silvery minnow is a small-bodied (<80 mm standard length) and short-lived (Horwitz et al., 2018) member of the family Cyprinidae (Table 1). This species has characteristics of both opportunistic (*e.g.*, rapidly maturing and short-lived) and periodic (*e.g.*, synchronous spawning) life histories (Fig. 1). Before the 1950s, Rio Grande silvery minnows were widespread and abundant in the Rio Grande and Pecos River from Northern New Mexico to the Gulf of Mexico in Texas (Treviño-Robinson, 1959; Pflieger, 1980; Hoagstrom, et al., 2010a). Extirpation of Rio Grande silvery minnow from the Pecos River was attributed to the introduction of its congener, plains minnow (*Hybognathus placitus*) (Moyer et al., 2005; Hoagstrom et al., 2010b). In the Rio Grande, major dam construction began in the early 1900s followed by construction of levees, smaller water storage dams, diversions, and flood control structures in the 1950s. Together, these structures result in an estimated 95% loss of instream flow and peak runoff in the Rio Grande compared to values expected if no regulation had occurred (Blythe and Schmidt, 2018). Extensive river regulation and channel drying in recent decades led to habitat degradation and extirpation of the species from >90% of its former range (U.S. Fish and Wildlife Service, 2010). Existing water rights and requirements for water delivery stipulated in interstate and international agreements currently limit opportunities for guaranteeing instream flows, especially during hot, dry summers. The current distribution of Rio Grande silvery minnow is a 280-km reach of the Rio Grande (U.S. Fish and Wildlife Service, 2010) and the species is listed as endangered (USFWS, 1994).

3.2. Reproductive ecology

Rio Grande silvery minnow is a member of the pelagophilic reproductive guild described by Balon (1975, 1981). Rio Grande silvery minnow produces non-adhesive, semi-buoyant eggs that remain in suspension as long as current is present (Platania and Altenbach, 1998). In captivity, females produce from ~2000 eggs (age-1) to ~10,000 eggs (age-4) (Caldwell et al., 2019). Spawning is synchronous and triggered by environmental cues (Platania and Altenbach, 1998) associated with elevated stream discharge during snowmelt runoff and rainstorm events that occur in the spring. These events increase water velocities, inundate floodplain habitats, and cause changes in water chemistry (Dudley et al., 2018b). River currents disperse drifting eggs and larvae both laterally and downstream (Dudley and Platania, 2007). A highly-modified water discharge regime and habitat changes increase the potential for extensive transport of Rio Grande silvery minnow eggs (Hoagstrom, 2014) to downstream sections of the river where mortality is high. Unassisted upstream movement is blocked by diversion dams. Periods of flow intermittency (*i.e.*, channel drying) now occur almost annually in the Rio Grande and strongly curtail recruitment and decimate adult populations (Archdeacon, 2016). Hence, interactions of reproductive ecology, short lifespan and current environmental conditions, cause densities of Rio Grande silvery minnow to vary by orders of magnitude across years, and recruitment failure in some years (*e.g.*, Dudley et al., 2018a).

Rio Grande silvery minnow is effectively an annual species so in the absence of intervention consecutive droughts cause population collapse (Horwitz et al., 2018). A key illustration of this dynamic is provided by considering October Rio Grande silvery minnow estimated densities which declined 99.6% between 2017 and 2018 due to poor spring runoff in 2018 (Dudley et al., 2018a). To mitigate extinction risk, a supportive breeding program was initiated in 2002 to supplement the wild population of Rio Grande silvery minnow (U.S. Fish and Wildlife Service, 2010). This program is now a cornerstone of recovery efforts with approximately 2.8 million individuals released to the middle Rio Grande (U.S. Fish and Wildlife Service, 2018, Appendix A) since inception. The program aims to increase survivorship of the most vulnerable life stages (eggs/larvae). Other goals are to (1) decrease the threat of extinction by bolstering the wild population, (2) buffer the species against genetic losses during years of failed wild recruitment, and (3) maintain refugial broodstocks reared from wild-caught eggs at multiple facilities and representing several year classes (U.S. Fish and Wildlife Service, 2010).

3.3. Incorporating wildness into hatchery and supplementation activities

The Rio Grande silvery minnow supportive breeding program was founded with ~922,000 fertilized eggs collected from natural spawning in the middle Rio Grande in 2003. Eggs are now collected at sites spanning the species' current range and temporal extent of spawning (typically May–June). Wild-caught egg or young-of-year collections (F_0) and captive spawning of fish reared from wild-caught eggs (F_1) are used to produce fish for supplementation (U.S. Fish and Wildlife Service, 2018). Annual egg collections are highly dependent on the size of the breeding population and magnitude of spring flows; hence, collections have ranged from zero (*e.g.* 2008–2009, 2019) to >825,000 (2006) since program inception (K. Ward, pers. comm.). In years when spring snowmelt runoff is poor, river flows can be manipulated to elicit spawning and facilitate egg collection. Wild-collected eggs/young-of-year are reared at conservation hatchery facilities until irrigation diversions cease in autumn. A portion of these fish are retained as broodstock. Higher genetic diversity of stocks reared from wild-caught eggs (Osborne et al., 2012) resulted in prioritization of these fish for stocking, broodstock development and maintenance. Fish reared spend less than six months in captivity and contribute to the middle Rio Grande breeding population the following spring. These strategies may reduce the opportunity for domestication selection but not eliminate it entirely. Captive spawning of Rio Grande silvery minnows is also necessary because of the highly stochastic and unpredictable nature of water availability, short duration of spawning, and short lifespan of individuals. Captive spawning involves randomly selecting an equal number of males and females and allowing them to mate freely within their group (Osborne et al., 2013; U.S. Fish and Wildlife Service, 2018).

Stocking densities for Rio Grande silvery minnow supplementation activities are based on *catch-per-unit effort* (CPUE) data derived from the Rio Grande silvery minnow population monitoring program (Dudley et al., 2018a) and observed occupancy within a reach (U.S. Fish and Wildlife Service, 2018, Appendix A). Stocking of a site is only undertaken if fewer than half the sites are occupied, or if reach average CPUE falls below 1.0 fish/m^2. This strategy allows supplementation efforts to be curtailed in years of strong natural recruitment.

Genetic monitoring has been conducted annually for the wild Rio Grande silvery minnow population since 1999, and for wild-caught fertilized eggs and offspring from captive spawning released to the Rio Grande since program inception (Osborne et al., 2012; Fig. S1). A 20-year time series shows that genetic diversity is maintained despite Rio Grande silvery minnow being virtually eliminated from the Rio Grande multiple times (*e.g.*, 2003, 2012–2014, Dudley et al., 2018a; Fig. S1C). More specifically, 'natural-origin' samples collected after the onset of population supplementation have greater microsatellite diversity and mitochondrial diversity than those obtained prior to supplementation. Genetic data indicates that supportive breeding and supplementation buffers the population against loss of genetic diversity following population bottlenecks.

4. Synthesis

Strict use of traditional captive breeding approaches, whereby individuals are spawned and their progeny reside in hatchery environments from the egg stage to release, have well-documented negative effects on wild fish populations (*e.g.*, Ford, 2002; Christie et al., 2012). However, hatchery rearing is necessary to prevent extinction for many species under existing biological and socio-political conditions (Naish et al., 2007). Programs highlighted here were developed and refined using extensive biological information, and adaptive, data-driven approaches (*e.g.*, Crossman et al., 2011a; Marsh et al., 2015; Minckley et al., 2003; Osborne et al., 2013). Collectively, they aim to minimize residence time in captivity and incorporate large numbers of 'natural-origin' individuals to ameliorate negative hatchery effects and facilitate recruitment. Programs were designed individually for each species. As adults, these fish occupy different ends of the life history spectrum, yet all three programs converge where egg/larval/juvenile mortality is high through impacts of biotic or abiotic factors (*e.g.*, non-native predators, river drying, degradation of spawning habitat, river fragmentation). Each program prioritizes breeding in the wild so that important behaviors (*e.g.*, mate choice, spawning habitat selection) can occur. In the case of Rio Grande silvery minnow, where spawning in captivity is unavoidable when spring flows or population densities are low, equal numbers of males and females are allowed to spawn in an aggregation such that mate choice can occur. Genetic data from Rio Grande silvery minnow suggested that neither fecundity nor neutral genetic diversity metrics differed between strategies and egg viability was significantly greater in the environmentally-cued design than the alternatives (Osborne et al., 2013).

Conservation hatchery protocols employed here were designed to accomplish genetic and demographic goals simultaneously by producing sufficient individuals to maintain levels of genetic diversity, preserve variation in life-history traits, and enhance survival of released fish relative to wild counterparts. Fig. 5A–C illustrate that each program has been successful over a 20-year period (1 to 20 generations) in maintaining (presumptively) neutral genetic variation, and relatively high effective breeding population sizes each year. The latter metric indicates a large proportion of spawning adults are represented in the offspring pool ensuring sufficient additive genetic variation in progeny (*e.g.*, Dammerman et al., 2015, 2016).

Neff et al. (2011) suggested that focusing solely on maintenance of neutral genetic variation may fail to account for components of fitness such as local adaptation and gene complementarity that are maintained by adult mate choice. Therefore, allowing natural mating (either in the wild or in captivity) is important because numerous studies have shown that mate choice is highly adaptive (*e.g.*, reviewed in Neff et al., 2011). Capturing progeny after natural spawning events allows adults to respond to environmental spawning cues, select mates and spawning substrate, while also subjecting fertilized eggs to natural environmental regimes before exposure to a novel hatchery environment. Exposure of individuals to natural environmental conditions during critical early ontogeny periods has long-term individual fitness consequences (concept of ontogenetic contingency; Diggle, 1994). Environmental exposure during early life has been shown to have effects on behavior (including migration timing), physiology, developmental rates, morphology and may have epigenetic benefits (Orizaola et al., 2010; Huey et al., 2012; Crespi and Warne, 2013; Pittman et al., 2013; Dammerman et al., 2015; Dammerman et al., 2016; Jonsson and Jonsson, 2014; Jonsson and Jonsson, 2019).

Sampling schemes for capturing eggs and larvae are designed to encompass biologically relevant temporal, spatial, and physicochemical variation in natural spawning conditions. For example, lake sturgeon is philopatric and imprints on local water chemistry and conditions. Hence, collections are made at the local watershed scale to ensure fish are exposed to appropriate cues that facilitate adult return to spawning localities. Drift nets are employed downstream of known spawning aggregations and drifting larvae are collected nightly. Larvae are retained each night in proportion to their relative abundance by hour and by night of return for subsequent hatchery rearing and eventual release. Sampling is also conducted for the entire reproductive season. Employing such tactics ensures a high total number and effective numbers of adults contributing to a diverse larval pool (Duong et al., 2013; Dammerman et al., 2019). Heritable variation in body size has been documented during the larval/juvenile period (Dammerman et al., 2015; Dammerman et al., 2016), but there is no direct evidence of domestication selection during hatchery residence. To minimize selection for spawning time or location, razorback sucker larvae are obtained from five spatially distinct and important spawning grounds that cover most of the upper portion of Lake Mohave. Sampling is conducted weekly at spawning localities from January to April. Rio Grande silvery minnow eggs are obtained using egg collectors that are moved periodically to ensure sampling across the species geographic range. Egg collections typically commence in May and continue through June but are timed to coincide with warming water temperatures, spring snowmelt runoff and rainstorm events. Rio Grande silvery minnow are released from captivity as maturing juveniles in November after the threat of stream drying has abated. By employing sampling regimes tailored to species-specific life histories, these conservation programs may maintain variation in key traits like spawning time and geographic variation in spawning conditions, and also maximize the number of parents contributing to the captive stock if conducted correctly. Genetic monitoring is used as a tool in each of the programs to assess whether genetic variation is being maintained.

Captive rearing of lake sturgeon, razorback sucker and Rio Grande silvery minnow results in exposure to different environments than wild counterparts. In captivity, individuals could experience either positive selection for hatchery conditions or relaxed natural selective pressures as they are reared and maintained. The opportunity for selection to occur in captivity, varies among species because of life history differences and threats they face. For example, razorback sucker is held longer than both Rio Grande silvery minnow and lake sturgeon. For Lake Mohave, razorback sucker is kept in captivity for several years until they reach about 450 mm in length to reduce predation by fish including striped bass and birds (*e.g.*, cormorants). At this size, males are mature and females are nearly mature and capable of reproduction the following season. Lake sturgeon and razorback sucker are released as juveniles or maturing adults because they are less susceptible to predation and can obtain sufficient resources to survive and recruit. There are potential negative impacts to this strategy. For example, female razorback suckers typically grow faster than males (McCarthy and Minckley, 1987); therefore, stocking larger individuals could potentially bias sex ratios. There is indirect and direct evidence that repatriated fish representative of the original source population, survive and reproduce (Dowling et al., 2005, 2014; Marsh et al., 2015; Carson et al., 2016). Yet, it is unclear how average fitness of repatriates compares with wild counterparts. Unfortunately, in circumstances involving endangered species (*i.e.*, Rio Grande silvery minnow and razorback sucker) direct comparisons of 'wild' and 'natural-origin' progeny is precluded as there are few or no 'wild' fish left for comparison of parameters or traits (*e.g.*, neutral genetic diversity, growth rate, body size, *etc.*) that may reflect fitness differences. In these situations, we can only assess survivorship in 'natural' conditions and how this affects the status of impacted populations/species.

Rio Grande silvery minnow spend a short time in captivity yet the potential for domestication selection is still present. Steps are taken to reduce hatchery selection these include rearing in outdoor ponds with natural photoperiod and temperature regimes, and deriving all broodstock from wild-caught eggs or juveniles. Direct comparison of fitness of released and wild individuals is not currently feasible, there is evidence however, that released fish contribute substantially to natural recruitment in the river. Specifically, (i) population monitoring data indicates tagged (hatchery) individuals are encountered in similar numbers, times and locations as untagged (wild) fish in the months preceding spawning (*e.g.*, Platania et al., 2020), (ii) values of gonadosomatic indices (relative weight of gonads to body weight) indicates comparable timing of reproduction of tagged and wild fish (T. Archdeacon pers. comm.), (iii) the average size of tagged fish is not significantly different from wild fish, (iv) persistence of the species despite wild population collapse in 2012–2014, 2018, and (v) maintenance of genetic diversity despite repeated population crashes (Osborne et al., 2012, Fig. S1C).

Lake sturgeon, razorback sucker, and Rio Grande silvery minnow conservation programs are employed to allow individuals to fulfill parts of natural life-cycle in their native habitats without compromising genetic diversity. For lake sturgeon, measures of genetic diversity in stream-collected larvae are significantly higher than offspring produced from direct gamete takes or from naturally produced eggs (Crossman et al., 2011a). Also, larval growth and survival is higher in streamside hatcheries when compared to traditional hatchery facilities (Crossman et al., 2011a). Genetic diversity was maintained in razorback sucker and Rio Grande silvery minnow populations (Fig. S1B and C) for >20 years despite ongoing threats to wild populations. Together, these disparate case studies demonstrate that rearing and supplementation programs can be tailored to species with very different adult life histories. Concepts, practices and procedures developed in these case studies and other innovations could be extended to conservation programs for imperiled fishes that require hatchery interventions (Anders, 1998; Paragamian and Beamesderfer, 2004), provided there is sufficient understanding of life history, habitat requirements, and impediments to recruitment.

Monetary costs, logistical constraints, or knowledge gaps may limit adoption of strategies outlined here. For example, collection of eggs or larvae may not be sustainable in cases where remnant wild populations occupy ecologically sensitive habitats (*e.g.*, Pahranagat chub, *Gila jordani*) and may be too difficult across all occupied habitats (*e.g.*, riverine populations of razorback sucker). Likewise, single-species collections of drifting eggs or larvae may be precluded when other coexisting species share reproductive biology (*e.g.*, broadcast spawning) and coincident reproductive timing. Other examples include species where locations of eggs or larvae are not known (*e.g.*, paddlefish, *Polyodon spathula*), where phenotypic development is highly sensitive to environmental differences such as temperature (*e.g.*, Devil's Hole pupfish, *Cypinodon diabolis*) or in situations where threats to recruitment and survival of adults in the wild cannot be ameliorated (*e.g.*, bonytail chub, *Gila elegans*). Finally, program implementation requires broader stakeholder engagement and participation when compared to traditional hatchery programs. Wider adoption of these strategies should increase overall success of conservation hatchery programs by allowing fishes to complete some part of the life-cycle in their natural habitats. Implementation will also improve understanding of species life-history, and provide an incentive to protect the native habitat such that habitats can ultimately support self-sustaining populations. Strategies outlined here could be extended to other imperiled fishes and are likely to minimize the impacts of domestication selection and other negative ecological or evolutionary outcomes of hatcheries while retaining their benefits.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108768.

Uncited references

Berejikian et al., 1996
Forsythe et al., 2012b

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We gratefully acknowledge the Michigan Department of Natural Resources, the Great Lakes Fishery Trust, and U.S. Fish and Wildlife Service for funding lake sturgeon hatchery research and the U.S. Bureau of Reclamation for funding razorback and Rio Grande silvery minnow research programs. We thank the many students, technical workers and agency biologists who have worked on and supported lake sturgeon, razorback sucker, and Rio Grande silvery minnow projects. Special thanks are extended to E. Baker, J. Bauman, N. Barton, and D. Larson, and to A. Snyder (UNM Museum of Southwestern Biology Division of Fishes) for curatorial support, to P. Marsh and B. Kesner for sharing extensive knowledge of razorback sucker biology and T. Archdeacon, K. Lang and K. Ward for sharing knowledge and unpublished data on Rio Grande silvery minnow and to W. H Brandenburg for permission to use illustrations of Rio Grande silvery minnow and razorback sucker in Fig. 1.

Data availability statement

Data will be deposited datadryad.org pending acceptance of the manuscript.

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